Mechanisms and mitigation of food web change in stream ecosystems

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Abstract

Freshwater ecosystems reflect the condition of their surrounding landscape, and thus are particularly vulnerable to anthropogenic stressors associated with human land-use. One of the most prevalent stressors on stream ecosystems in agricultural regions, such as the Canterbury Plains of New Zealand, is eutrophication, or increased primary productivity. The aim of this thesis was to investigate effects of eutrophication on stream communities, specifically food web structure and ecosystem function. From a food web perspective, eutrophication is a shift in the form and amount of available energy from externally-produced (allochthonous) to internal (autochthonous) basal resources. Such shifts are frequently associated with land-use intensification, due to riparian vegetation removal and increased nutrient inputs, both of which enhance autochthonous production. A field survey across a gradient of eutrophication showed that eutrophic stream food webs are largely autochthonously-based and often contain large numbers of defended primary consumers, which form trophic bottlenecks and prevent energy from reaching higher trophic levels. Consequently, while there is more total energy available, less of that energy is in a usable form for stream food webs. Moreover, I found that eutrophic streams are largely composed of generalist consumers, which shift their diets to refocus on autochthonous resources with increasing productivity. Given that eutrophication causes food web resources to become more homogenous and was a primary driver of food web change, I tested whether reintroducing allochthonous subsidies would alter or reverse the negative effects of eutrophication. To do this I conducted a short-term community assembly experiment and a year-long population biomass accrual study. I found that the simplified, generalist-dominated communities in eutrophic streams did not respond to changes in resource diversity as predicted by food web theories, which are based on more diverse food webs. After restoration of allochthonous subsidies, defended generalist taxa continued to dominate the invertebrate communities. However, while restoring allochthonous subsidies did not mitigate the numerical dominance of defended consumers, the biomass accrual of other, previously excluded desirable taxa, such as mayflies and predatory invertebrates, increased following resource additions. This indicates that more energy reached the top of the food web, suggesting that resource additions alleviated trophic bottlenecks. Overall, my findings have advanced current knowledge about key mechanisms driving food web responses to both anthropogenic stress and to restoration efforts, which can be applied to improve management and restoration of stream ecosystems.

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1

Introduction

Ecosystems worldwide are under mounting stress as a result of expanding human populations and human impacts, such as global climate change, accelerated rates of biological extinctions and invasions, habitat fragmentation, and land-use alterations (Vitousek *et al.* 1997; McCann 2000; Sala *et al.* 2000). Therefore, one of the most pressing challenges for ecologists today is to understand how human activities are affecting ecosystem biodiversity, structure, function, and stability to develop management strategies for mitigating negative effects (Foley *et al.* 2005), restore degraded ecosystems to a healthier state (Lake *et al.* 2007), and more accurately predict ecosystem responses to future impacts (Chapin *et al.* 2000; Dangles *et al.* 2011). My goal for this thesis was to help address these challenges in freshwater ecosystems.

Freshwater habitats and biodiversity are especially vulnerable to anthropogenic changes, and biodiversity declines have been larger and more rapid in freshwaters than in any other ecosystem type (Ricciardi & Rasmussen 1999; Sala *et al.* 2000; Dudgeon *et al.* 2006). Freshwater ecosystems are disproportionately affected by human impacts both because they have been a focus for human settlement and thus heavily exploited (Malmqvist & Rundle 2002), and because they ultimately receive and reflect the consequences of any disturbance or alteration within their catchments (Hynes 1975; Allan 2004). Catchment land-use change, particularly agricultural development, is a leading driver of biodiversity change in freshwater ecosystems (Sala *et al.* 2000), and has been associated with multiple deleterious effects on freshwater ecosystems, including declines in stream water and habitat quality, increased temperatures, increased nutrient and sediment loads, and eutrophication, or extreme increases in ecosystem productivity (Harding *et al.* 1999; Quinn 2000; Allan 2004; Allgeier *et al.* 2011; Burdon *et al.* 2013).

New Zealand is no exception to this global trend (MacLeod & Moller 2006). The Canterbury Plains region in particular has undergone extensive agricultural development in the last two decades, largely due to the intensification of dairy farming (MacLeod & Moller 2006; Pawson & Holland 2008), and current projections by both the dairy industry and the New Zealand Parliamentary Commissioner for the Environment indicate that expansion will continue to increase for at least another ten years (PCE 2004; MacLeod & Moller 2006). Furthermore, many of the small streams that cross the Canterbury Plains, which have the potential to be reservoirs of biodiversity (Ver-

donschot *et al.* 2012), have become inextricably mixed into a network of agricultural drains and irrigation or stock water races (Winterbourn 2008; Greenwood *et al.* 2012). A thorough investigation of the impact of agricultural development on freshwater ecosystems is therefore increasingly necessary for effective management of water resources in New Zealand and world-wide.

My specific aim for this thesis was to examine how agricultural land-use intensification is affecting the diversity, function, and stability of stream communities on the Canterbury Plains. I evaluated the influence of eutrophication as a symptom representing agricultural impact; eutrophication is an increase in trophic state, or increase in primary productivity, of an ecosystem. Eutrophication is often linked to agricultural development, as both nutrient enrichment from fertilizer or animal run-off and removal of adjacent vegetation, which increases temperature and light availability for photosynthesis, result in greater in-stream primary productivity (Quinn 2000; Hagen *et al.* 2010). Thus, eutrophication represents both landscape and in-stream changes.

Eutrophication can also interact with other agricultural stressors, either additively or antagonistically (Matthaei *et al.* 2010). For example, high sediment loads increase turbidity, which can decrease light availability for photosynthesis and thus decrease algal growth (Niyogi *et al.* 2007). Sediment deposition can also restrict physical access to algal biofilms by stream biota (Niyogi *et al.* 2007). Clearing of riparian vegetation may increase stream temperatures, which have been linked to shifts in stream invertebrate community composition (Parkyn *et al.* 2003; Quinn *et al.* 2004). Disturbance has also been shown to interact with stream productivity by reducing algal growth (Tonkin *et al.* 2013) and favoring superior colonisers instead of superior competitors (Kondoh 2001). In an effort to isolate and focus on the effects of eutrophication alone, only low sediment and low disturbance streams were chosen as study sites for this thesis.

I used food webs to investigate the effects of eutrophication on stream communities, because food webs integrate community structure, including diversity and composition, with energy flow and trophic dynamics (Winemiller & Polis 1996; Tunney *et al.* 2012). I wanted to identify the mechanisms driving relationships between productivity, diversity, and ecosystem processes, and improve our understanding of community and food web response to eutrophication. Identifying these mechanisms will advance general ecological theory and aid managers in devising strategies for the maintenance of healthy and functional stream ecosystems.

Eutrophication of freshwater ecosystems

Eutrophication alters the form and amount of energy available to organisms (Dodds 2007). Freshwater organisms, particularly in streams, rely on a mixture of internal (autochthonous) and externally-produced (allochthonous) food resources (Cummins 1975). Autochthonous production consists of algae and aquatic plants (macrophytes), whereas allochthonous inputs include terrestrial leaf litter or other detritus (Cummins 1975). When a catchment is converted to agricultural land-use, the balance between autochthonous and allochthonous production is disrupted, as allochthonous resources often decline due to removal of vegetation while nutrient enrichment and the loss of canopy cover stimulate in-stream autochthonous growth (Quinn 2000; Hagen *et al.* 2010). Thus, eutrophic streams have increased productivity, or available energy, but only in a single form. Resource homogenization has been linked to altered community composition; for example, commu-

nities shift from detritivore dominance in forested headwaters to herbivore dominance in large, open, downstream reaches (Vannote *et al.* 1980). Some organisms, on the other hand, can adjust their diet to match changes in resource availability (Finlay 2001). As community composition and/or consumption patterns shift, trophic interactions may also change, further altering energy flow within an ecosystem (Leibold 1999; Davis *et al.* 2010). Thus, understanding the effects of increasing productivity on stream ecosystems will be crucial in designing mitigation or restoration strategies for waterways in areas undergoing agricultural land-use intensification.

Productivity-diversity relationships

The effect of increases in ecosystem productivity on ecosystem inhabitants, particularly the diversity of species, is a long-standing unresolved question in ecology (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hillebrand & Cardinale 2010). Although it was originally assumed that higher productivity would support more species (Connell & Orias 1964), mathematical models predicted the opposite. Later empirical tests had mixed results, and currently both the shape and direction of the relationship between productivity and diversity remains uncertain (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hillebrand & Cardinale 2010). Yet it is even more important to unravel, as agricultural expansion will continue to increase with rising global food demand (Tilman *et al.* 2011), hastening ecosystem degradation.

Influence of diversity on ecosystem function and stability

Preserving biodiversity is critical not only as an end in itself, to prevent losses of unique species, but also because biodiversity in turn has important influences on ecosystem function and community stability (McCann 2000; Naeem 2002; Hooper *et al.* 2005). Multiple ecosystem functions and community stability are enhanced by high diversity and reduced by declines in diversity (McCann 2000; Hooper *et al.* 2005). In this context, 'diversity' can be used specifically to refer to species richness, the number of different taxa present, or it can be used more broadly to include species composition, such as relative abundance or evenness. It can also refer to functional diversity, in which organisms are classified and grouped by functional traits (Reiss *et al.* 2009), or characteristics determining how an organism interacts with other organisms or its environment (Hooper *et al.* 2005). Which of these aspects of diversity determine biodiversity-ecosystem function relationships remains unclear. However, several studies have indicated that community composition is as equally important as species richness as a predictor of ecosystem function (Hooper *et al.* 2005). Ecosystem function refers to the natural processes that contribute to self-maintenance of an ecosystem, such as formation of biomass, carbon storage, nutrient cycling, decomposition, and transport of sediment or other materials (Thompson *et al.* 2012). Sometimes a single numerically dominant species can provide the majority of a certain ecosystem function (Smith & Knapp 2003; Doherty *et al.* 2011), while in other situations rarer species, such as top predators, can have a disproportionately large effect (Woodward 2009). In either situation, greater diversity improves the chances key taxa are present (Hooper *et al.* 2005).

Biodiversity likewise benefits stability, the capacity of ecosystems to persist under stress or dis-

turbance (Rooney & McCann 2012), because species respond differently to disturbance or perturbation; thus, the more species which are present, the more likely it is that if one species is lost, another will be able to fulfill the same role (Naeem 2002; McCann 2000). Again, whether species diversity, functional diversity, or composition is more critical for stability remains to be thoroughly tested (Wellnitz & Poff 2001; Steiner *et al.* 2005).

A new approach to old questions – food webs

The majority of previous productivity-diversity and diversity-ecosystem function studies have focused on a single trophic level, usually autotrophs, and occasionally their direct consumers, omitting higher trophic levels (Thompson *et al.* 2012). Including additional trophic levels is likely to generate more complex responses (Hooper *et al.* 2005; Thébault & Loreau 2006), and several experiments report that diversity at different trophic levels is influenced by different mechanisms (Longmuir *et al.* 2007; Yee *et al.* 2007; Korhonen *et al.* 2011), and may not respond to increases in productivity in the same way, or have equal influence on ecosystem functions (Woodward 2009). Moreover, interactions between organisms, including predator-prey relationships, as well as facilitation and/or competition, may further modify diversity relationships (Thébault & Loreau 2006; Rooney & McCann 2012). Food webs incorporate these complexities by combining diversity/composition and trophic interactions into a network of energy flow (Thompson *et al.* 2012).

The network structure of food webs is likely to provide valuable information about community response to stress. For example, changes in composition or diversity will affect the number of nodes within a food web, while changes in trophic interactions, including consumption or competition, will be represented as shifts in the number and/or position of links within the web (Olesen *et al.* 2010). Stress at any level of the network is liable to affect populations and linkages elsewhere in the web. Food web topology, including width, height, and distance between nodes, is also influenced by environmental conditions; as a result, food webs expand or contract in response to ecosystem changes (Tunney *et al.* 2012). Consequently, a food-web perspective is a very useful framework for testing the mechanisms driving the relationships between productivity (and associated changes in resource availability), diversity, and ecosystem function and stability in eutrophic streams. In this thesis, I applied a food-web approach to test the mechanisms by which eutrophication affects stream ecosystems.

Thesis structure and chapter outlines

This thesis has been written as a series of stand-alone papers which will be submitted for publication. As a result, there is some repetition of material, particularly methods, between chapters, although I have tried to minimize this by referencing earlier chapters where possible.

The first half of the thesis was designed to identify and clarify the mechanisms driving productivity-diversity relationships, while the second half focused on applying the results to stream restoration. Chapter Two documents a survey of eighteen streams across a gradient of increasing productivity. I examined changes in benthic macroinvertebrate and fish community composition, diversity, and trophic interactions across a productivity gradient. Productivity-diversity relationships were de-

termined for each trophic level individually and compared to the whole community relationship. I used gut contents analysis of predators to elucidate trophic interactions. To further investigate the effects of productivity and changing community composition on trophic interactions, I also constructed productivity-diversity relationships for groups of taxa based on different functional traits, such as presence/absence of morphological defences (*i.e.* shells or hard cases).

In Chapter Three, I tested whether resource diversity drove the productivity-diversity relationships observed in Chapter Two, because previous studies have reported significant correlations between resource diversity and consumer and predator diversity (Moore & Hunt 1988; Yodzis 1988). I used stable isotope analysis to study how the shift in resource diversity/availability along the productivity gradient affected food web structure via changes in consumption by various consumer groups. I then calculated isotopic metrics describing food-web structure for each stream to compare the influence of altered consumption patterns on food web structure along the productivity gradient. By constructing food webs in isotopic space using stable isotope signatures, I was able to test whether community composition or change in diet was the primary driver of community response to eutrophication.

Because Chapter Three indicated that resource availability and subsequent changes in consumption and trophic diversity affected food web structure, for the fourth chapter I conducted a short-term (six week) experiment which tested the effectiveness of restoring resource diversity, through reintroduction of allochthonous subsidies, for improving community diversity and evenness in eutrophic streams. Previous research in North America has shown, through exclusion experiments, that stream macroinvertebrate diversity and community composition are strongly linked to allochthonous resource availability (Wallace *et al.* 1999). To test this idea, resources were manipulated via shading and allochthonous resource additions at both small (patch) and large (stream reach) scales.

Chapter Five further investigated the effects of this allochthonous subsidy restoration over the course of one year using a before-after-control-impact (BACI) experimental design to evaluate the impact of the reach-scale addition. I monitored the effects of allochthonous subsidy additions on invertebrate diets, food-web structure and a key ecosystem function, secondary production of benthic macroinvertebrates. Secondary production is the formation of heterotrophic biomass by stream invertebrates, and describes energy utilization and transfer within an ecosystem (Benke 1993). Like diversity, secondary production can be strongly limited by allochthonous resource availability (Wallace *et al.* 1999). My BACI experiment tested whether restoring subsidies would in turn enhance ecosystem function, namely energy flow, throughout the food web.

Finally, in Chapter Six I summarise my results and outline how they add to our understanding of stream food-web structure and our potential to mitigate anthropogenic stresses such as stream eutrophication. I discuss the implications of my research for general ecological theory and what my results might mean for food-web stability and ecosystem function in eutrophic streams. I also propose new questions which build on my results, and suggest potential applications of my findings to stream management and restoration.

Each data chapter will be a co-authored publication, reflecting the contributions of others as outlined in the acknowledgements, but the majority of work, including analysis and writing, is my own. Figures and tables are numbered continuously throughout the thesis. A complete reference

list is provided at the end of the thesis, rather than for individual chapters. Several chapters have appendices to provide additional details, which will be included as supplementary materials to publications. Several chapters of this thesis also cite a paper, Burrell *et al.* (in press), on which I am a co-author. The measurements of stream metabolism (gross primary production, GPP) included in Chapters Two and Three were collected jointly by co-authors and calculated by Teresa Burrell for her MsC, and will be published in this paper in the January 2014 issue of *Freshwater Science*.

2

Community composition and trophic interactions influence productivity-diversity relationships in stream food webs

Abstract

The relationship between productivity and diversity is one of the oldest questions in ecology, and it is of increasing concern for freshwater ecosystems undergoing anthropogenic eutrophication and biodiversity losses. We investigated the relationships between primary productivity, diversity, and community composition in 18 streams across a eutrophication gradient in the South Island of New Zealand. We hypothesized that trophic levels would respond differently to enhanced productivity as a result of changes in community composition, and that it is the combination of multiple productivity-diversity relationships within a food web which creates the theoretically predicted unimodal relationship between productivity and diversity. Principal components analysis yielded two orthogonal axes of productivity, one associated with gross primary productivity (GPP) and the other with algal biomass (chlorophyll-*a*). The GPP axis was correlated with decreased richness of primary consumers, particularly pollution-sensitive taxa, but increased abundance of defended taxa, such as cased caddisflies and snails. The chlorophyll-*a* axis was correlated with increased richness of predatory invertebrates as well as increased richness and abundance of defended taxa. We found no relationships between primary productivity and richness or abundance of predatory invertebrates or fish, indicating that the increased productivity was not being passed up the food chain. The predominance of defended consumers in eutrophic streams is likely a trophic bottleneck; gut contents analysis indicated that both invertebrates and fish strongly prefer undefended prey, the availability of which decreased with productivity. Thus the productivity-diversity relationship is not a simple correlation, but consists of multiple consumer responses to multiple sources of productivity, mediated by trophic interactions. Consequently, managers need to focus on preserving food web structure as well as biodiversity, particularly preventing the loss of trophically important taxa to avoid trophic bottlenecks in eutrophic systems.

Introduction

"Something so pervasive ought to have a simple explanation" (Rosenzweig 1995). When Michael Rosenzweig wrote those words, the pervasive 'something' in question, the ecosystem productivity-species diversity relationship, had already been under investigation for thirty years (Hutchinson 1959; Connell & Orias 1964); today almost another twenty years of study have passed, yet the simple explanation remains elusive (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hillebrand & Cardinale 2010). The question itself, however, remains as important as ever, perhaps even more so, because human impacts are increasingly altering both the productivity (Dodds 2007; Hagen *et al.* 2010) and diversity (McCann 2000) of ecosystems. Humans have increased the productivity of land by modifying native vegetation, planting crops, and adding fertilizers (nutrients) to soils. Waterways are inextricably linked to their surrounding watershed (Hynes 1975; Allan 2004), so these modifications have also increased productivity of freshwater ecosystems, often resulting in eutrophication, or excess productivity (Dodds 2007). At the same time, biodiversity is declining worldwide at a more rapid rate than ever previously recorded (McCann 2000) and most rapidly in freshwater ecosystems (Dudgeon *et al.* 2006). Understanding the fundamental mechanisms controlling relationships between productivity and diversity is more critical than ever, to help us make accurate predictions about long-term or ecosystem-wide impacts of eutrophication, and manage ecosystems, particularly freshwaters, effectively to preserve biodiversity and sustain ecosystem functions.

Both theoreticians and empiricists concur that productivity affects diversity, but the direction and shape of the relationship remain under debate (Waide *et al.* 1999; Mittelbach *et al.* 2001; Hillebrand & Cardinale 2010). It was originally assumed that higher production would support increased diversity by reducing competition among organisms for resources (Hutchinson 1959; Connell & Orias 1964). Conversely, Rosenzweig (1971) reported a "paradox of enrichment," when analytical models of nutrient enrichment resulted in a loss, rather than an increase, in diversity, due to the increased competitive dominance of extremely efficient resource exploiters at high resource levels. Several early terrestrial experiments found declines in plant species diversity with increased fertilization, consistent with the paradox of enrichment (Brenchley & Warrington 1958). However, many subsequent studies reported a unimodal relationship between productivity and diversity, and it has been argued that linear relationships might reflect a failure to examine the full range of productivity, thereby missing the hump of the curve (Rosenzweig & Abramsky 1993). While a unimodal productivity-diversity relationship may be theoretically attractive, empirical results have been mixed, and we are still far from a clear general consensus (Rosenzweig & Abramsky 1993; Tilman & Pacala 1993; Rosenzweig 1995). It is even uncertain whether productivity regulates diversity and not vice versa (Cardinale *et al.* 2009).

Some of the confusion may stem from the theory itself being oversimplified; most productivity-diversity relationships were based on studies including only a single trophic level, autotrophs, and occasionally their direct consumers, which is rarely, if ever, the structure of a natural ecosystem (Polis & Strong 1996). However, the idea that changes in productivity will affect higher tropic levels, and even entire food webs, is not new. In trophic cascade theory, the abundance and biomass of trophic levels are regulated by the combination of bottom-up (resource) and top-down (preda-

tor) forces (Hairston *et al.* 1960; Power 1992). It has been suggested that such forces may also result in richness varying between trophic levels (Kneitel & Miller 2002; Yee *et al.* 2007), in which case there could be different productivity-diversity relationships for each trophic level. We hypothesized that it is the combination of multiple productivity-diversity relationships within a food web which creates the commonly observed unimodal curve. For instance, simultaneous positive and negative linear relationships could together generate a unimodal pattern, as in a subsidy-stress situation (Niyogi *et al.* 2007). The limited number of studies which have investigated productivity-diversity relationships for individual trophic levels have reported a variety of relationships (linear, unimodal, no relationship at all) for each trophic level, suggesting diversity at different trophic levels may be controlled by different mechanisms (Longmuir *et al.* 2007; Yee *et al.* 2007; Korhonen *et al.* 2011).

Shifts in community composition due to increasing primary productivity is one potential mechanism determining trophic level richness. For example, in streams, changes in macroinvertebrate community composition have been previously reported in conjunction with land-use change and associated nutrient enrichment, both of which stimulate stream primary productivity (Niyogi *et al.* 2007). In our stream study, we expected community composition would shift with primary productivity because some taxa and/or functional groups may benefit more from increased resources than others, due to feeding morphology, behavior and/or dietary preference (Winterbourn *et al.* 1984). For example, one primary consumer taxon well-suited to consumption of autochthonous production could out-compete and begin to exclude more generalist feeders (Holomuzki *et al.* 2010). Shifts in community composition will in turn affect trophic interactions. If the highly competitive taxon is significantly more or less attractive to predators, its increasing dominance could result in altered predation pressure on the other remaining primary consumers, *i.e.* apparent competition (Leibold 1996). Such changes in trophic interactions could then influence the richness, and thus the productivity-diversity relationship, of each trophic level through either bottom-up (prey composition effects on predator diversity) or top-down (predator composition effects on prey diversity) processes. Because our goal was to investigate possible ecosystem consequences of eutrophication, we focused on one-way relationships with primary productivity as the driver of diversity and not vice versa.

Methods

This study was conducted on eighteen streams in the Canterbury region of South Island, New Zealand (Figure 2.1). We conducted our study on stream food webs because freshwater ecosystems support multiple trophic levels (Polis and Strong 1996), are highly impacted by eutrophication (Allgeier *et al.* 2011), and are experiencing rapid declines in biodiversity (Dudgeon *et al.* 2006). Streams were first or second order, two to three meters wide, and were selected to encompass gradients of both catchment agricultural land-use intensity (and therefore nutrient concentrations) and riparian cover (*i.e.* shade), thereby spanning a large gradient of productivity. Furthermore, because high levels of fine sediment in agricultural catchments have been shown to have deleterious effects on stream communities, only streams with predominantly cobble bottoms were selected (Burdon *et al.* 2013).

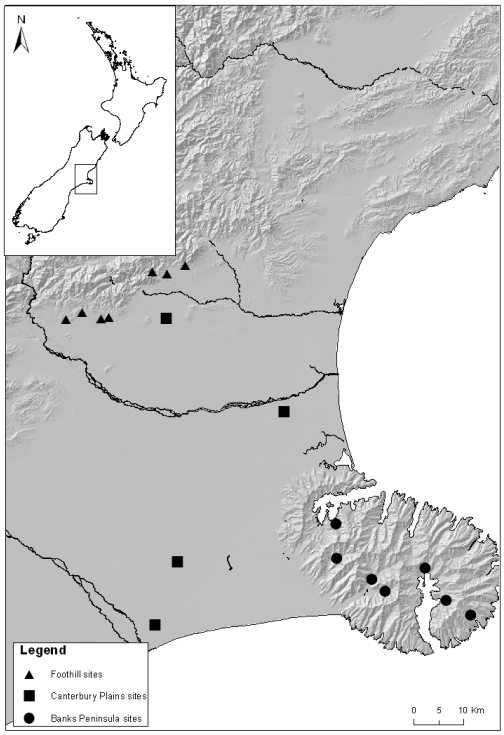

Figure 2.1: Location of 18 study sites within the Canterbury region, South Island, New Zealand. Canterbury Plains sites are represented by squares, Foothill sites by triangles, and Banks Peninsula sites by circles.

Sites were distributed among three sub-regions: the Canterbury Plains, Banks Peninsula, and Canterbury foothills. The Canterbury Plains are located between the eastern coastline and the Southern Alps on alluvial outwash plains of glacial origin (Webb 2008). Land use in the Canterbury plains is dominated by pastoral agriculture and intensive dairying (Pawson & Holland 2008) and introduced conifers are now the most common trees (Meurk 2008). The Banks Peninsula is a hilly region of volcanic origin; the steep slopes are composed of basalt and andesite, while loess deposits cover the low-elevation hills and valleys (Webb 2008). Pasture/grassland covers over half (approximately 64%) of the land area, and the majority of remaining tree cover is regenerated beech and podocarp forest (Wilson 2008). The Foothills region lies directly at the base of the Southern Alps, to the west of the Canterbury Plains. It is characterized by pallic or brown soils (Webb 2008) and mixed beech/conifer/broad-leaved forest (Burrows & Wilson 2008). Each region has a range of agricultural intensity and riparian coverage, therefore the productivity gradient in this study was not simply an artifact of regional differences (verified via Mantel test; see Appendix A).

Field and laboratory methods

Streams were sampled in the late austral summer (February to April) of 2010. Reach lengths ranged from 70 to 270 meters, and were scaled to width and discharge, with longer reaches for larger streams. Stream width and depth were measured at ten equidistant points across eight equally-spaced transects along each reach. The presence/absence and type of macrophyte cover

(submerged or emergent) was recorded at each point along the transects, and a bed particle was randomly selected and its width measured; these measurements were later added and averaged, respectively, to obtain percent macrophyte cover and mean particle size per site. Shade measurements were taken at the midpoint of each transect using a densiometer. Temperature was measured using D-Opto Loggers (Zebra-tech, Nelson, New Zealand), stream velocity was measured both upstream and downstream with a Marsh-McBirney Flo-Mate (Marsh-McBirney, Frederick, Maryland, USA) and stream discharge calculated using standard velocity integration (Gore 2007).

Four benthic macroinvertebrate samples were collected using a Surber sampler (25 cm x 25 cm, 250 μm mesh) from each stream reach following a stratified random design; the reach was split into five equidistant segments, and a randomly-generated list of possible one meter locations within each segment was used to choose sampling locations. At each location, the sample was taken in what was judged to be the best habitat for macroinvertebrates (*i.e.* cobble and riffle zones) within a one-meter radius of the designated point. If macrophyte beds were predominant habitat along the reach, at least two samples were taken from within the macrophyte beds. Invertebrates in samples were separated into two size classes using 500 μm and 250 μm nested sieves. If a sample contained more than 500 invertebrates, it was sub-sampled volumetrically (1/2, 1/4, or 1/8, depending on abundance of the full sample) and the invertebrate counts and biomass later scaled appropriately. Invertebrates from each size class were counted and identified under a stereomicroscope ($10 - 63X$ magnification; Nikon SMZ800, Melville, New York, USA) to the lowest practical taxonomic level: genus for mayflies, caddisflies, stoneflies, and snails; subfamily for flies and beetles; class for worms; phylum for nematodes and flatworms; family (bivalves) or genus (gastropods) for molluscs; and order (cladocera, amphipods) or subclass (copepods) for microcrustacea, using Winterbourn *et al.* (2006) and unpublished keys (B. Smith, NIWA, Hamilton, New Zealand). Biomass was determined using ash-free dry mass (AFDM); the sorted macroinvertebrates were dried at 50°C for at least 48 hours, weighed, ashed at 540°C for 4 hours, and then re-weighed. Diversity was calculated as rarefied species richness to allow comparison between streams of varying invertebrate abundance (Heck *et al.* 1975). Kicknet samples were also taken in all habitat types and frozen for later gut contents analysis.

Fish were sampled with a backpack electric fishing machine (Kainga 300 EFM, NIWA, Christchurch, New Zealand), and identified using McDowall (2001). Size (body length) and wet weights of each fish caught were measured in the field. Ten fish of each species (or fewer if less than ten were caught) per site were euthanized with phenoxyethanol, brought back to the laboratory, and frozen for later gut content analysis (Thompson *et al.* 2001).

In the gut contents analysis, fish and invertebrate stomachs were removed under a stereomicroscope ($10-63X$ magnification; Nikon SMZ800, Melville, New York, USA) and the contents identified to the lowest possible taxonomic level (genus for mayflies, caddisflies, and snails, family for flies, and class for microcrustacea) and counted. Prey selectivity was calculated as the log ratio of the relative proportions of various prey items present in the gut divided by the relative abundance of that prey item at the site (adapted from Chesson (1978)). The mean selectivity of each predator on each prey type was then ranked between 1 and 5, with 1 being strongly selected against and 5 strongly selected for. The rank for each prey item was multiplied by the abundance of that item at a site; the sums for each site were considered a measure of "community palatability" or suitable

prey availability for higher predators. Community palatability indices were calculated only for the three most abundant invertebrate predator taxa and the four most common fish species due to insufficient sample sizes for gut contents and regression analysis of less abundant organisms.

Production and respiration for each stream were measured using the one-station diurnal oxygen curve technique (Bott 2007). Oxygen concentrations were measured for a span of $2-5$ days at each site using D-Opto loggers (Zebra-tech, Nelson, New Zealand). To minimize variation in photosynthetic production due to cloud cover, loggers were not collected until there had been at least one clear day in the logging period. Production and respiration were calculated using the time series of oxygen concentration readings; daytime respiration was estimated as the average of post sunset (sunset-midnight) and predawn (midnight-dawn) respiration rates. Gross primary productivity was calculated as production minus respiration and re-aeration, which was measured by propane evasion at each site (Bott 2007; Burrell *et al.* in press); see A for further detail.

Algal biomass was measured from the biofilm of five large (fist-sized) cobbles collected at random intervals longitudinally within the stream reach. The cobbles were transported to the laboratory in the dark and on ice, and frozen. Algal chlorophyll-*a* was extracted using hot ethanol extraction (Sartory & Grobbelaar 1984); each cobble was immersed in a known volume of ethanol and placed in a water bath at 78˚C for 5 minutes, then removed and refrigerated in the dark for $12-18$ hours, at which point chlorophyll-*a* concentration in the ethanol extract was measured using a flourometer (Trilogy Laboratory Fluorometer, Turner Designs, Sunnyvale, California, USA). Chlorophyll-*a* concentration was multiplied by the surface area of each rock, which was calculated using three axis measurements (Graham *et al.* 1988), and the resulting chlorophyll-*a* per square meter measurement used as a surrogate for algal biomass (Steinman *et al.* 2007).

Nutrient concentration and uptake were measured using short-term additions of NH_4 and PO_4. A solution of NH_4 and PO_4 was continuously dripped into the stream using a peristaltic pump (target concentration = 15 μg/L) until plateau saturation ($2.5-3$ times travel time), at which point stream water samples were collected from eight equidistant points along the reach via syringe and filtered using GF/F filters (Whatman, GE Healthcare, Buckinghamshire, UK). Pre-samples were also collected prior to nutrient addition. All samples were stored on ice for transport to the laboratory, and frozen until analysis. Water samples were analyzed for nitrate and phosphate on an Easy-Chem Plus (Systea Scientific, Anagni, Italy) discrete auto-analyzer. Nitrate was measured via cadmium reduction and soluble reactive phosphate was measured using molybdate reduction (Eaton et al. 1995). Ammonium was measured using fluorometry (Holmes *et al.* 1999) on a Turner Trilogy (Turner Designs, Sunnyvale, CA).

Particulate organic matter (POM) was collected in the Surber samples and later separated from the invertebrates in the laboratory, and split into coarse ($> 500\mu$m) and fine (250μm to 500μm) size classes using nested sieves. Fine benthic organic matter (FBOM) was sampled using the stovepipe corer method, in which a PVC tube was inserted into the streambed and the sediment within stirred up by hand, at three locations: upstream, midway, and downstream, along the stream reach. The samples were filtered (GF/F filters, Whatman, GE Healthcare, Buckinghamshire, UK) in the laboratory. All particulate organic matter samples were dried at 50˚C for at least 48 hours, weighed, ashed at 540˚C for 4 hours, and then re-weighed to determine the mass of both organic and inorganic particulate material.

Statistical Analysis

To determine the shape of relationships between various measures of primary productivity and diversity, we had to identify how each set of variables changed across the land-use/eutrophication gradient and in relation to each other. First, we investigated patterns in community composition and changes in diversity metrics across sites. Secondly, we determined which primary productivity variables were responsible for most environmental variation. Thirdly, we calculated prey selectivity of predators for various prey based on their gut contents, then generated a total selectivity score, or community palatability index, for each stream. Finally, we tested for relationships between productivity, community richness and composition, and community palatability.

A non-metric multidimensional scaling (NMDS) ordination was used to assess community structure and evaluate drivers of distribution between sites. The NMDS was undertaken with the 'vegan' package (Oksanen *et al.* 2012) in R (R Development Core Team 2010), using the metaMDS function with a Bray-Curtis dissimilarity matrix on untransformed invertebrate abundance data for each site. The metaMDS is an iterative analysis in which several random starts are used to reach better confidence of the final configuration. To achieve best fit, the metaMDS was run twice, with the second run starting from the solution of the first run.

To begin, we created separate NMDS plots for the macrophyte and non-macrophyte samples from sites containing both habitat types to test for within-stream effects of habitat on community composition. We compared the two ordinations using an analysis of similarity (ANOSIM), also using the 'vegan' R package (Oksanen *et al.* 2012). The ANOSIM indicated that community composition did not vary significantly between habitat types (Figure A.1), although macrophyte habitats supported higher invertebrate abundances. Therefore counts from all samples were combined for each stream, and the total counts for each taxa were adjusted by the percent of macrophyte habitat within each stream. The corrected abundances were used to run a final NMDS for all sites.

Linear trends, or vectors, were then fit to the NMDS using the envfit function; envfit finds the direction in ordination space towards which a vector changes most rapidly, indicating greatest correlation with the ordination configuration, or change in community. Various diversity and community composition metrics were tested in the vector analysis, such as richness and abundance of individual trophic levels as well as of pollution- and/or disturbance-sensitive EPT (mayfly, stonefly, and caddisfly) taxa, a common measure of stream invertebrate health and diversity. All richness measures were rarefied to account for varying sample sizes using the rarefy function in package 'vegan' in R. The significance of fitted vectors was assessed using a permutation test (Oksanen *et al.* 2012). We used the vectors to identify which aspects of community structure varied significantly between sites, and should therefore be included as individual response variables in later analyses.

To account for cumulative and/or interactive effects of multiple productivity factors, a principle components analysis (PCA) was used to create composite axes encompassing the majority of variation in primary productivity across sites. Environmental variables hypothesized to affect productivity, including shade, macrophyte cover, particle size, nutrients (nitrate and ammonium), chlorophyll-*a*, productivity (GPP), heterotrophic respiration, and POM, were included

in the PCA. Phosphate was excluded from the analysis because of naturally high phosphate levels in the volcanic soils of the Banks Peninsula. Variables were log-transformed when necessary to meet assumptions of normality. The PCA was run in R using the 'prcomp' function; variables were scaled to have unit variance through division by the root mean square prior to analysis. Variables with PCA loadings > 0.7 were considered significant environmental factors.

Regression analysis was used to test the relationships between the environmental (PCA) axes and the community variables that were significant vectors in the NMDS. To expand our examination of potential compositional changes, we also included total biomass and average individual mass (abundance divided by biomass) of each trophic level and defended/undefended consumer groups as response variables. The best model fit for each pair of variables was determined by using AIC_c to compare linear and nonlinear (quadratic) regressions both with and without GPP-chlorophyll-*a* interaction terms. The best model from the AIC_c was then tested with partial regression analysis to minimize covariance effects between the two measures of productivity. Partial regression tests the relationship between two variables (for example richness and chlorophyll-*a*) while holding a third variable (GPP) constant by plotting the residuals of the regression between the response variable and the constant explanatory variable against the second explanatory variable (Kurle & Cardinale 2011). Although response variables were inherently collinear (biomass is correlated with abundance, and average mass is the ratio of abundance to biomass), we present them individually because the risk of Type II errors is low. The relationships between richness of trophic levels were tested with linear regression. Variables were log-transformed (abundance, biomass, average mass) or square-root transformed (richness) to meet assumptions of normality.

Analysis of variance (ANOVA) followed by Tukey multiple comparisons of means was used to test for differences in selection between defended, undefended, and predatory invertebrate (i.e. intraguild predation for predatory invertebrates) prey for both invertebrates and fish. Relationships between productivity and community palatability (the summed selection scores) were then determined using the AIC_c and partial regression procedures described above.

Results

All streams were first or second order, mostly cobble-bottomed, with a median width of 2.7 m (range 1.1 − 7.6 m) and a median depth of 12 cm (range 7 − 37 cm). Discharges ranged from 3 L/s to 590 L/s, with a median of 24 L/s. Ranges and means of all measured environmental and community variables are given in supplementary Table A.1.

The NMDS ordination vectors of invertebrate communities indicated that gradients of community structure were primarily characterized by differences in species richness and abundance (Figure 2.2; see A.2 for vector analysis). The vectors for total community richness, primary consumer richness, and EPT richness were all positively aligned with the first NMDS axis. The abundance of primary consumers was associated with the opposite end of the same axis, indicating that when abundance was high, diversity was low; *i.e.* the increase in abundance is not community-wide, but likely due to increases in one or few consumer groups. To further investigate this dominance by a subset of primary consumers, we classified primary consumers into two groups, those with morphological defenses (*e.g.* caddisflies that have hard cases or snails with shells) and those without.

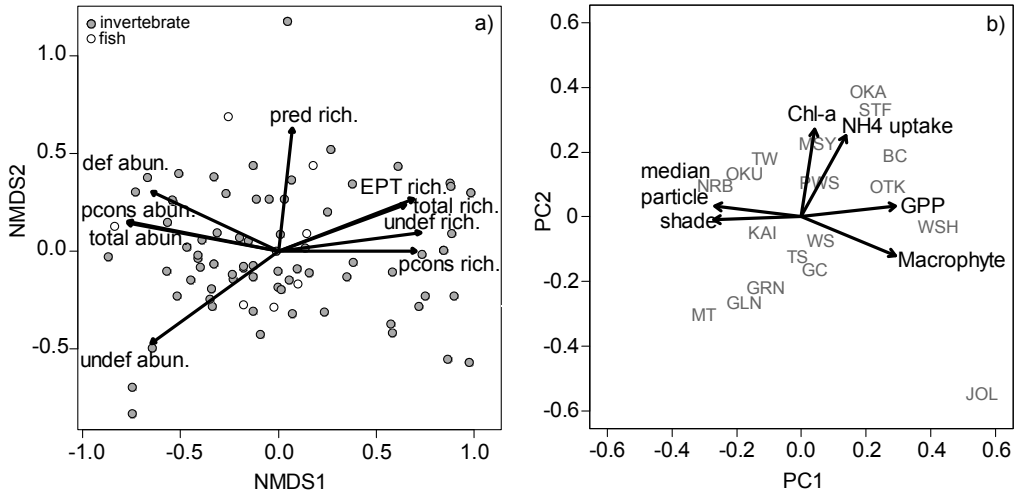

Figure 2.2: a) Non-metric multidimensional scaling (NMDS) ordination of invertebrate and fish abundances and b) Principal components analysis (PCA) of environmental variables across 18 streams in the Canterbury region, South Island, New Zealand. The two NMDS axes represent gradients in community composition between sites. Points are individual taxa; the distance between points reflects how frequently those taxa co-occur. Arrows on the NMDS ordination are fitted vectors for community metrics; the direction and length of arrow represent the direction and strength of correlation with the ordination. Abbreviations are as follows: abun - abundance; rich - species richness; def - defended primary consumers (i.e. with shells or hard cases); pcons - primary consumers; undef - undefended primary consumers (without hard shells or cases); EPT - pollution-sensitive indicator taxa, Ephemeroptera, Plecoptera, and Trichoptera. Each PCA axis represents an environmental gradient, and arrows show variables with axis loadings > 0.7, indicating that they were clearly associated with an axis; the direction of the arrow denotes the direction of correlation. Points are individual sites as indicated by site name labels. The full site names are given in Table 3.2. The variables included in the PCA analysis are listed in the methods, abbreviations are as follows: Chl-a - chlorophyll-a, an estimate of algal biomass; GPP - gross primary production, a measure of stream metabolism; macrophyte - percent coverage by aquatic plants (macrophytes); median particle - median bed substrate size; NH_4 uptake - ammonium uptake; shade - percent canopy cover.

The richness of undefended consumers was negatively correlated with the first NMDS axis, while the abundance of both defended and undefended groups was positively related to that axis. The only vector aligned with the second NMDS axis was predator richness, suggesting that predator diversity is not linked to primary consumer diversity or abundance.

The PCA yielded two orthogonal environmental gradients, which together explain 60% of the variance in the productivity-related environmental data (Figure 2.2; see Table A.3 for variable loadings). The first axis (44% of the variation) was negatively associated with gross primary productivity (GPP) and macrophyte cover, and positively correlated with shade and median particle size. These associations indicate that streams with low axis one scores had high macrophyte coverage and high GPP, while streams with larger axis one scores were characterized by high shade and large cobble size. The second axis (16% of the variation) was negatively associated with chlorophyll-*a* and NH_4 uptake rate (Table A.3), indicating that streams with low axis two scores had high concentrations of chlorophyll-*a* (*i.e.* high algal biomass) and faster ammonium uptake. The first and second PCA axes will hereafter be referred to as the GPP axis and the chlorophyll-*a*

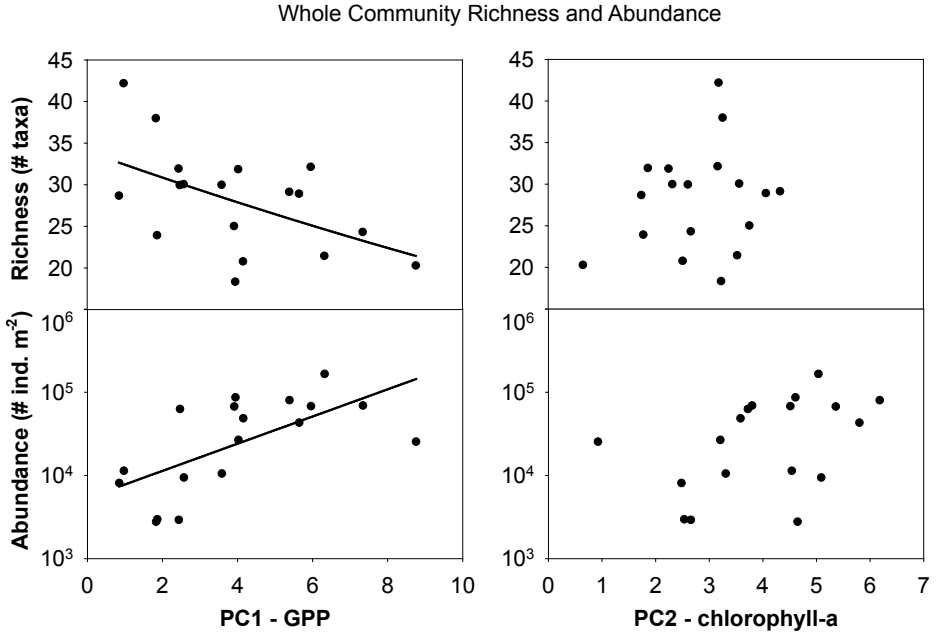

Figure 2.3: Community richness and total abundance in each of the 18 sites across the two productivity axes. Richness values were rarefied based on the smallest sample size. Abundance is reported as density, or number of individuals per square meter, and includes both invertebrates and fish. Lines indicate significant linear regressions at $P < 0.05$.

axis, respectively.

Contrary to our predictions, there were few significant differences in fit ($\Delta AIC_c > 2$; Anderson & Burnham (2002)) between linear and unimodal models for the relationships between productivity and community variables; when differences were significant, the linear models were a better fit (Table A.4). Given that our GPP measurements varied by two orders of magnitude and our algal biomass measurements by one order of magnitude across sites, we are confident that our gradients span the full range of productivity and our models did not exclude potential humps in the curve. The interaction term between GPP and chlorophyll-*a* was not significant in any of the models tested, indicating that community metrics were associated primarily with one productivity axis or the other. Partial regression did not change the conclusions drawn from ordinary linear regression (Table A.5), therefore we present the standard regression plots.

Productivity-diversity relationships varied between trophic levels and sources of productivity. We found a negative linear relationship between overall community richness and productivity, not the expected unimodal relationship (Figure 2.3, GPP: $F_{1,16} = 4.77$, $P < 0.05$, $R^2 = 0.23$). Nonetheless, our hypotheses that trophic levels would respond differently to change in productivity and that species composition would shift with productivity were supported, albeit in a more complex fashion than we predicted due to the multiple productivity axes.

Richness and abundance of different groups were associated with one or both of the productivity gradients. The richness of the majority of primary consumer groups was associated with the GPP axis. As GPP increased, the richness of undefended consumers and EPT taxa declined (Figure 2.4, undefended consumer richness: $F_{1,16} = 11.5$, $P < 0.01$, $R^2 = 0.42$; EPT richness: $F_{1,16} = 28.2$, $P < 0.01$, $R^2 = 0.64$). The abundance of both defended and undefended primary

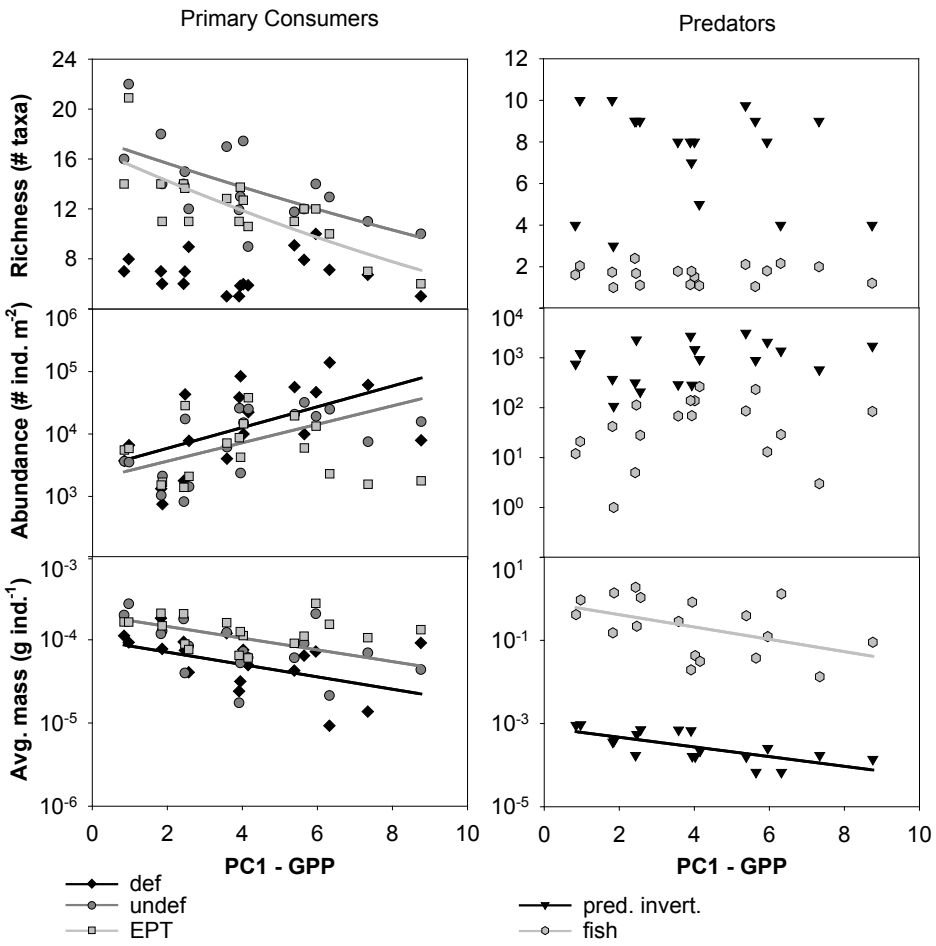

Figure 2.4: Richness, abundance, and average mass of primary consumer groups, predatory invertebrates, and fish across the gross primary productivity (GPP) gradient. Abbreviations are as follows: def - defended primary consumers with hard cases, such as caddisflies, or shells, like snails; undef - undefended consumers without cases or shells; EPT - taxa sensitive to pollution, includes families Ephemeroptera, Plecoptera, Trichoptera; pred. invert. - predatory invertebrates, fish - fish. Lines indicate significant linear regressions at $P < 0.05$.

consumers, on the other hand, increased along the GPP axis (Figure 2.4, defended: $F_{1,16} = 7.14$, $P < 0.05$, $R^2 = 0.31$; undefended: $F_{1,16} = 9.54$, $P < 0.01$, $R^2 = 0.37$). Although abundances increased, biomass did not increase correspondingly across either productivity gradient (regression plots not presented). Consequently, the average mass of both defended consumers and undefended consumers declined along the GPP gradient (Figure 2.4, defended: $F_{1,16} = 5.08$, $P < 0.05$, $R^2 = 0.24$; undefended: $F_{1,16} = 4.65$, $P < 0.05$, $R^2 = 0.23$), indicating that while there were more individuals, they were smaller. This was most likely due to an increase in the relative abundance of smaller taxa, rather than a decrease in individual size of taxa. Average masses of predatory invertebrates and fish also decreased with increasing GPP (Figure 2.4, predatory invertebrates: $F_{1,16} = 15.94$, $P < 0.01$, $R^2 = 0.50$; fish: $F_{1,16} = 4.58$, $P < 0.05$, $R^2 = 0.22$), again suggesting a shift towards numerical dominance of smaller species at high productivity. In fact, the lack of any relationships (richness, abundance, biomass) between higher trophic levels and either of the two productivity axes is in itself important; it indicates that the increased primary production was not

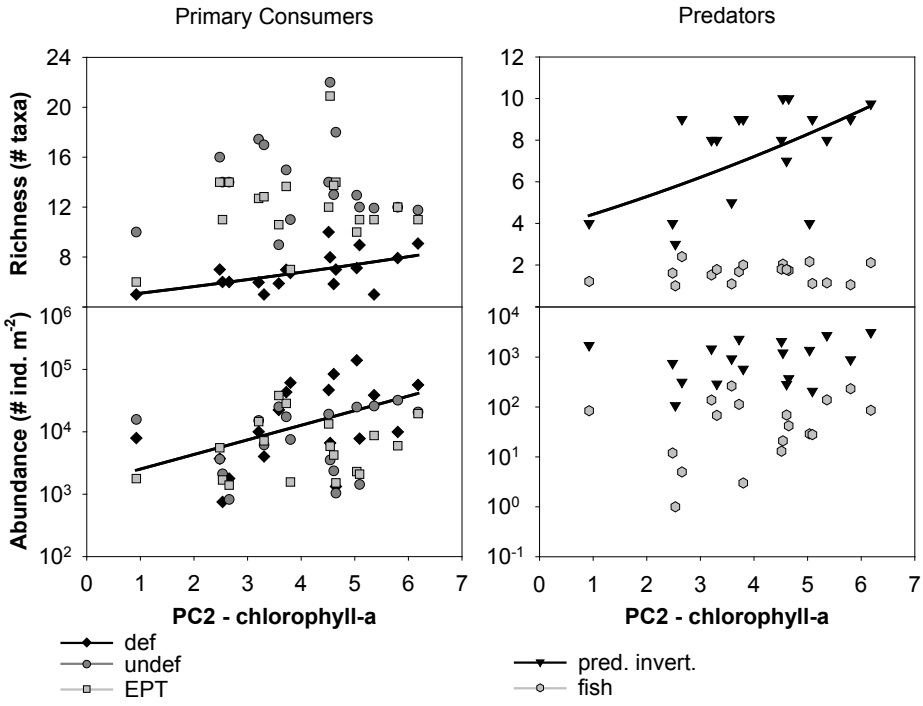

Figure 2.5: Richness and abundance of primary consumer groups, predatory invertebrates, and fish across the chlorophyll-*a* gradient. Abbreviations are as described for Figure 2.4. Lines indicate significant linear regressions at $P < 0.05$.

making it up the food web, despite corresponding increases in prey abundance.

The chlorophyll-*a* axis was associated with the richness of defended consumers and predatory invertebrates; both had greater richness at high productivity (Figure 2.5, defended: $F_{1,16} = 4.63$, $P < 0.05$, $R^2 = 0.22$; predatory invertebrates: $F_{1,16} = 7.03$, $P < 0.05$, $R^2 = 0.31$). Defended consumers were the only group to increase in abundance along this gradient, perhaps indicating smaller shifts in community composition in comparison to the GPP gradient. There were no changes in biomass or average mass for primary consumers, predators, or fish with increasing chlorophyll-*a* (regression plots not presented).

Fish species richness did not vary significantly with either productivity axis (Figure 2.4, GPP: $F_{1,16} = 0.003$, $P > 0.10$, $R^2 = 0.0002$; (Figure 2.5, chlorophyll-*a*: $F_{1,16} = 0.19$, $P > 0.10$, $R^2 = 0.01$). Moreover, the richness of the three trophic levels were not correlated with each other (Figure A.2, predatory invertebrates-primary consumers: $F_{1,16} = 2.66$, $P > 0.10$, $R^2 = 0.14$; fish-predatory invertebrates: $F_{1,16} = 2.35$, $P > 0.10$, $R^2 = 0.13$; fish-primary consumers: $F_{1,16} = 1.75$, $P > 0.1$, $R^2 = 0.10$).

The prey selectivity calculated based on predator gut contents indicated that both predatory invertebrates and fish preferentially fed on undefended rather than defended prey (Table 2.1). There were significant differences in selection between the three prey types by predatory invertebrates ($F_{2,31} = 26.0$, $P < 0.001$). All preferred undefended to defended prey, although *Stenoperla* had the least difference in selection between the two, and *Archichauliodes* preferred other predatory invertebrates the most. Fish also had significant selection differences between prey types ($F_{2,13} = 8.62$, $P < 0.01$). All species selected predatory invertebrates most strongly but varied in their selection

Table 2.1: Prey selection scores for each predator. Selection was calculated as the log ratio of relative abundance of a prey item in a predator's stomach divided by the relative abundance of that prey item within a site. Scores were assigned a rank from 1 (least preferred) to 5 (strongly preferred).

		defended		undefended		pred. invert.	
Predator	n	mean log ratio	rank	mean log ratio	rank	mean log ratio	rank
Invertebrates							
Archichauliodes	10	-0.03	3	0.55	4	1.98	5
Hydrobiosidae	32			0.74	4		
Stenoperla	6	0.35	4	0.45	4		
Fish							
Canterbury galaxias	29	-0.09	3	0.11	3	1.35	5
Brown trout	26	-0.47	2	-0.12	3	1.56	5
Longfin eel	39	-0.54	2	0.46	4	2.2	5
Upland bully	100	-0.22	3	0.11	3	1.55	5

of defended and undefended prey. There was a significant difference in selection between small fish (Canterbury galaxiids and upland bullies), which had intermediate selection (neither strong for or against) toward defended prey, and large fish (brown trout and longfin eels), which selected against defended prey ($F_{1,24} = 4.45$, $P < 0.05$).

The community palatability indices (the sum of mean selection for each taxa multiplied by the relative abundance of each taxa at a site) also differed between small and large fish, while there was no significant correlation between community palatability and either productivity axis for any of the predatory invertebrates. Community palatability decreased linearly (see Tables A.6 and A.7 for AIC_c and partial regression analyses) with increasing GPP for brown trout and longfin eels (Figure 2.6, brown trout: $F_{1,16} = 9.37$, $P < 0.01$, $R^2 = 0.37$; longfin eels: $F_{1,16} = 9.80$, $P < 0.01$, $R^2 = 0.38$), indicating that the relative availability of their preferred prey declines at high productivity. The lack of change in index scores for Canterbury galaxiids and upland bullies across the GPP gradient suggests that they are not as strongly affected by the shifts in primary consumer composition associated with increasing productivity, perhaps due to their greater tolerance for defended prey. In fact, the palatability score for upland bullies increased with chlorophyll-*a* (Figure 2.6, $F_{1,16} = 3.75$, $P = 0.07$, $R^2 = 0.19$); bullies were the only species that had any change in palatability scores across that gradient. Again, this indicates that bullies may not only be unaffected by, but may possibly benefit from, an increase in defended consumers, unlike the larger fish species.

Discussion

Unraveling the mechanisms behind productivity-diversity relationships is of critical importance, as it is unlikely that the current trend of urbanization and agricultural conversion will slow, let alone stop or reverse, in the near future (Brussaard *et al.* 2010), and both biodiversity declines (McCann 2000) and eutrophication of aquatic and terrestrial systems will continue to be global concerns (Allgeier *et al.* 2011). In our investigation of productivity-diversity relationships in stream food webs, we observed that streams can have multiple sources of productivity which affect various components of the food web differently, in contrast to the single-cause and single-effect re-

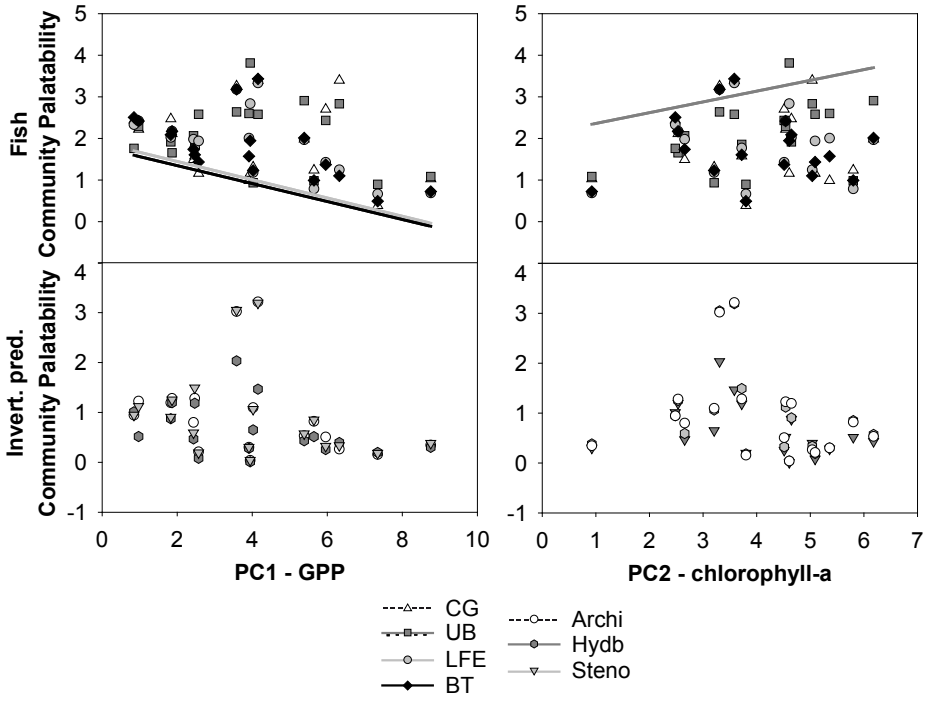

Figure 2.6: Community palatability scores for fish and predatory invertebrate diets across the two productivity gradients. Palatability scores represent the sum of selection values for each predator on each prey type, calculated as the log ratio of the abundance of a prey item in the predators' gut contents to the relative abundance of that prey within a site. A higher score denotes increased availability of preferred prey. The gross primary productivity (GPP) gradient is plotted in the first column and the chlorophyll-*a* (*i.e.* algal standing stock) gradient is shown in the second. Palatability indices for fish are shown in the top row. Abbreviations for fish are as follows: CG - Canterbury galaxids; UB - upland bullies; LFE - longfin eels; BT - brown trout. Invertebrate palatability indices are shown in the bottom row. Abbreviations for predatory invertebrates are as follows: Archi - *Archichauliodes*; Hydb - Hydrobiosids; Steno - *Stenoperla*. Solid lines indicate significant linear regressions.

lationship associated with most productivity-diversity theory (Rosenzweig & Abramsky 1993). We found that changes in primary consumer community composition were driven by increasing productivity and influenced both top-down and bottom-up trophic interactions. Changes in composition and trophic interactions were in turn associated with differences in richness between trophic levels. These results demonstrate how a food-web approach can help resolve some of the confusion surrounding productivity-diversity relationships.

While other studies have reported that species richness was correlated with different abiotic environmental factors, such as geographical location, elevation, temperature, and light, between trophic levels (Longmuir *et al.* 2007; Korhonen *et al.* 2011), our study highlights the importance of different types of productivity. Traditionally in productivity-diversity theory it has been assumed that commonly used measures of productivity and diversity, including surrogate productivity values such as precipitation (in terrestrial ecosystems) or standing biomass, were mechanistically equal and/or interchangeable (Mittelbach *et al.* 2001). Yet in our study two of the most frequently employed measures in aquatic ecosystems, chlorophyll-*a* and gross primary production (GPP), were driven by different autotrophic components of the ecosystem (algae and aquatic

macrophytes, respectively), evidenced by their separation on two orthogonal axes in a principal component analysis of productivity variables. Macrophytes, which are abundant in stable agricultural streams due to stable flows and high light availability, were the primary contributor to GPP in our sites. However, macrophytes are not readily incorporated into aquatic food webs, except as detritus (Hamilton *et al.* 1992), and may serve more as a structural/habitat resource. For example, bottom-dwelling defended consumers, such as *Potamopyrgus* snails, typically feed on the epiphytic algae growing on the macrophytes rather than the macrophyte tissues themselves (Collier 2004; Jaschinski *et al.* 2011). By contrast, algal biomass is immediately available as a food resource to the stream food web and is limited primarily by nutrients and light, which are abundant in our eutrophic study sites. Disturbances, such as floods, can also influence algal biomass but are rare in our spring-fed lowland agricultural streams (Biggs & Close 1989). While both algal biomass and GPP are appropriate and representative measures of ecosystem productivity, they represent fundamentally different sources of energy and should not be assumed to be equivalent.

Our results indicate that distinguishing between productivity sources may be an important first step in clarifying the mechanisms driving productivity-diversity relationships. Multiple sources of productivity are actually the norm for most ecosystems (Olff *et al.* 2009). For example, lake food webs contain both benthic and pelagic production (Vadeboncoeur *et al.* 2003), while savannah food webs have both grasses and woody trees at the base (Olff *et al.* 2009). Furthermore, the majority of ecosystems also contain a detrital component which is frequently overlooked in productivity and/or food web studies (Moore *et al.* 2004). It is especially important to consider multiple sources of productivity in food web analyses because different types of productivity may be associated with specific and separate components of the food web (Vadeboncoeur *et al.* 2003; Olff *et al.* 2009). For example, we found that primary consumers were largely associated with GPP, except for defended taxa, which, along with predatory invertebrates, were associated with chlorophyll-*a*. Furthermore, average masses of both undefended and defended taxa declined with GPP, suggesting a compositional shift towards small-bodied organisms, which may benefit more from or be able to respond more quickly to increased productivity due to faster population turnover (Korhonen *et al.* 2010). Such results begin to explain why previous productivity-diversity studies have often yielded conflicting conclusions; if ecosystems have multiple sources of productivity, each affecting community composition differently, then multiple productivity-diversity relationships, potentially of different shapes and in opposite directions, can occur simultaneously.

Although each productivity source (GPP and chlorophyll-*a*) was linked with different trophic levels and food web components (*i.e.* defended and undefended consumers), changes in community composition associated with one productivity source impact other groups not directly associated with that productivity type through trophic interactions (Worm & Duffy 2003). Changes in species composition associated with increased productivity can influence trophic interactions in multiple ways. For example, across the GPP gradient we observed declines in richness of undefended taxa and EPT, but increases in abundance of both undefended and defended taxa. The decline in richness of other groups in conjunction with increased abundance (and no loss of richness) of defended consumers suggests that either of two possible mechanisms is in effect. First, competitive exclusion could be occurring. If the defended consumers are more efficient at maximizing their consumption on autochthonous production, they could reduce the availability of food,

habitat, or other resources to their competitors (Figure 2.7). Both herbivorous snails and cased larval caddisflies, which were the two most abundant and ubiquitous defended consumers in our streams, are known to be strong algal exploiters. *Potamopyrgus* snails have been reported to reduce grazing rates of other less competitive species (Holomuzki *et al.* 2010). Secondly, apparent competition could be taking place, if the increase in abundance of defended taxa, which are less palatable and attractive to predators (Nystrom *et al.* 2003), indirectly increases the predation pressure on the undefended taxa (Holt 1977) (Figure 2.7). In fact, consumer competition models predict that predator-resistant taxa should dominate at high productivity (Leibold 1996). The decline in richness and lack of increase in abundance of EPT taxa with GPP suggests that they are potentially the most vulnerable to either exclusion or predation, or both. However, given their status as pollution sensitive organisms, it is also possible their decline is related to an external/environmental variable associated with increasing productivity that was not measured directly in this study. For example, Niyogi *et al.* (2007) reported declines in EPT richness and abundance with increasing agricultural impacts, particularly the covering of benthic habitats with fine sediment.

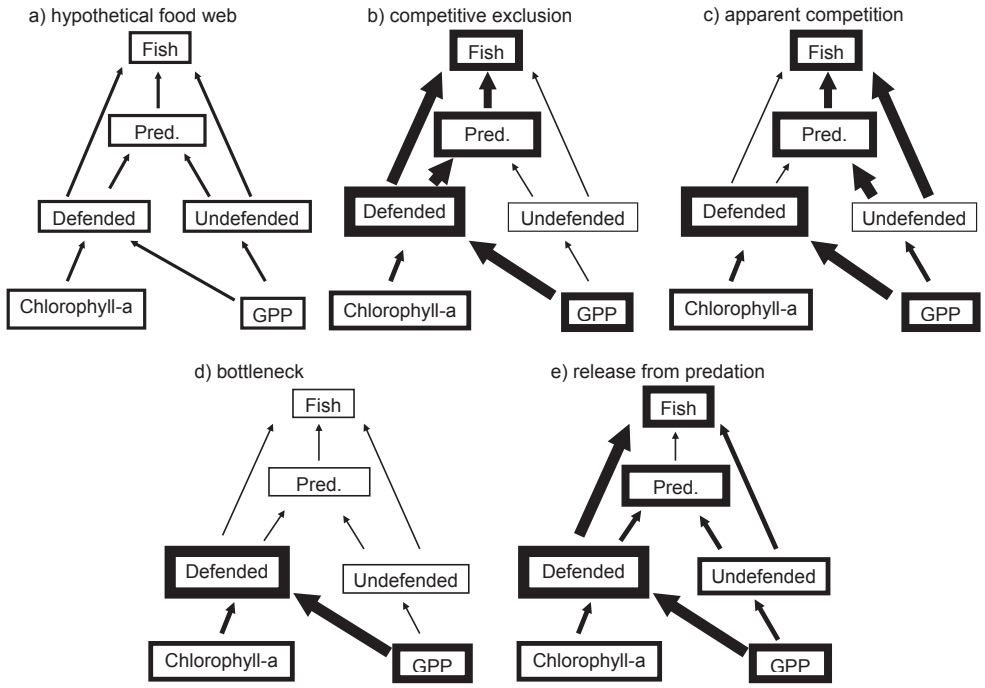

Figure 2.7: Conceptual diagrams of trophic interactions hypothesised to be associated with increasing productivity: a) food web before changes in productivity; b) food web with competitive exclusion between defended and undefended primary consumers; c) apparent competition operating on undefended consumers; d) trophic bottleneck created by defended consumers, e) release of predatory invertebrates from fish predation. Black lines represent energy flow upward through the food web, the width of the arrows indicate the amount of energy flow. Likewise, the width of the box around each consumer indicates the amount of energy being stored in that compartment.

We cannot determine from our study which of these mechanisms is responsible for the observed changes in community composition, but it is clear that shifts in composition altered trophic interactions. The increases in primary consumer (defended and undefended taxa) abundance suggest

a bottom-up effect of productivity (Connell & Orias 1964). However, there were no increases in abundance, or biomass of predatory invertebrates or fish, indicating that while more energy was available, it was not being passed up to higher trophic levels. We suspect the greater abundance of defended consumer taxa along the GPP gradient is largely responsible for the observed lack of increase in richness or abundance of higher trophic levels. If predators avoid defended taxa, the increased energy coming into the bottom of the food web becomes trapped in unpalatable primary consumer biomass, creating a trophic bottleneck which prevents predator populations from expanding correspondingly to the increase in productivity at the base of the food web (Davis *et al.* 2010) (Figure 2.7). Our gut contents analysis supports this conjecture, as both predatory invertebrates and fish were found to prefer undefended consumers as prey.

The chlorophyll-*a* axis, on the other hand, was not associated with bottom-up effects. As algal biomass increased, defended consumer richness and abundance also increased, as did predatory invertebrate richness. This pattern was surprising because the gut contents analysis indicated that the predatory invertebrates were still selecting against the increasingly abundant and diverse defended consumers. This seemingly counterintuitive result suggests that a top-down mechanism may be at work instead, such as released predation pressure from fish (Hairston *et al.* 1960) (Figure 2.7). A similar top-down effect was reported by Kneitel & Miller (2002), who found that addition of a top predator which reduced bacterial-feeding rotifer populations was associated with increases in bacterial species richness. In our study the release was not brought about by the addition of a higher trophic level, but a switch in diet of the existing predators. The increase in community palatability score across the chlorophyll-*a* gradient indicates that upland bullies switched to consuming more of the increasingly abundant defended prey, especially snails, in high productivity sites, potentially reducing predation pressure on predatory invertebrates.

The mechanisms discussed in the previous paragraphs and illustrated in Figure 2.7 demonstrate how community composition influences trophic interactions, and vice-versa, within a food web, resulting in different productivity-diversity relationships at different trophic levels. The negative correlations between primary consumer richness and GPP were likely due to antagonistic interactions among primary consumers, while higher trophic levels did not increase in richness and abundance as expected because of a bottleneck. The positive correlation between predatory invertebrate richness and algal biomass was potentially due to a reduction in top-down control by fish. Interestingly, empirical results are split on whether richness of trophic levels are correlated. Two similar studies of productivity-diversity relationships of phytoplankton, zooplankton, and bacteria systems in lakes reported opposite results; Korhonen *et al.* (2011) found correlations in richness between trophic levels, while Longmuir *et al.* (2007) found no evidence of feedbacks between trophic levels. In our study, we also found that richness of trophic levels were not related, indicating that the relationships we observed between productivity and richness of trophic levels are co-occurring independently.

Our results demonstrate that productivity does not affect biodiversity directly; its impacts are determined by associated changes in trophic interactions and community composition. The productivity-diversity relationship is not a simple correlation, or even a single correlation, but a complex aggregate response mediated by different sources of productivity, changes in community composition, and interactions between organisms at different trophic levels. As a result, productiv-

ity-diversity relationships can be positive, negative, unimodal, or perhaps even a variety of other shapes (Waide *et al.* 1999; Mittelbach *et al.* 2001), depending on the species composition (Fukami & Morin 2003) and which interactions dominate in a given ecosystem.

The next step in designing effective management and/or restoration strategies for impacted ecosystems is to determine the relative role of species composition in determining the productivity-diversity relationship. For example, in a laboratory experiment using freshwater microbes, Fukami & Morin (2003) found that altering the order of community assembly resulted in many differently-shaped productivity-diversity curves between communities all containing the same species. Biodiversity-ecosystem functioning studies have also begun to question the relative importance of composition versus diversity. Several studies have reported that community composition had a greater effect on ecosystem functioning than overall richness particularly the presence of competitive dominants or keystone species (Cardinale *et al.* 2000; Downing & Leibold 2002; Dangles & Malmqvist 2004). Further experimental manipulations of community composition are required to compare productivity-diversity relationships among communities of equal richness but varying composition. Our research indicates that it will be necessary to incorporate the effects of species' traits which modify trophic interactions into compositional analyses as well. In addition, it will be important to determine which trophic interactions are changing, how they in turn affect community composition and richness, and whether there are potential feedback loops (Worm & Duffy 2003). If community composition and trophic interactions can be regulated to control productivity, there may be exciting new possibilities for integrated food web-ecosystem management of eutrophication. For example, top predator additions have been used in lakes to stimulate trophic cascades in which algal grazer abundance increases, thus reducing algal biomass (Carpenter *et al.* 2001). Increasing the abundance of native predators which select for defended consumers, such as upland bullies, could potentially achieve similar results for stream food webs by eliminating the bottleneck and reducing competitive exclusion/apparent competition on other primary consumers, thereby restoring community evenness and maintaining trophic links.

3

Food-web structure and resource use, but not trophic height, shift across a gradient of stream eutrophication

Abstract

There is a pressing need to improve understanding of how anthropogenic changes affect key ecosystem services. Food webs offer a promising framework to accomplish this because they summarise energy flow through communities. We investigated the links between resource availability, resource use, and food-web structure across a gradient of eutrophication, encompassing 18 streams in the Canterbury Plains region of South Island, New Zealand, using isotopic metrics of food web structure and dietary mixing models. The gradient incorporated forested and open streams flowing through a range of agricultural intensity, from protected reserve land to dairy farms. Gross primary productivity ranged between $0.04 - 2.78$ g $O_2/m^2/day$, and was linked to altered food-web topology associated with changes in resource availability along the gradient. All consumers had elevated autochthonous contributions to body mass (indicated by carbon isotope signatures) with increasing productivity, which led to horizontal expansion of food webs within isotopic niche space. Overall trophic diversity (number of niches) increased across the gradient, probably because our streams contained trophic generalists capable of switching between allochthonous and autochthonous resources. Trophic redundancy, on the other hand, declined with productivity, indicating that the differences in diet switching between generalist taxa pushed them apart in niche space. We did not find a corresponding increase in trophic height, suggesting the increased autochthonous energy was not reaching higher trophic levels. Gut contents analysis of predators did not indicate prey selection based on energy source of prey, although preferred prey groups were relatively less abundant in high productivity sites. The decline in trophic redundancy and increased reliance on a single resource with increasing productivity indicates potential for increasing food web instability with eutrophication. Understanding how resource availability and consumption affect food web structure and stability will aid managers in predicting and mitigating potential effects of eutrophication on stream communities. We recommend that increasing resource diversity will create more diverse food webs, enhance food-web stability, and possibly reduce trophic bottlenecks in eutrophic streams.

Introduction

Food webs integrate the combined effects of changing landscapes (Allan 2004), habitat conditions (Sponseller *et al.* 2001), and community composition (Thompson & Townsend 2004), and reflect patterns in both species diversity and trophic interactions (Tunney *et al.* 2012). Therefore, food webs are a powerful tool to better understand and guide management of anthropogenic impacts on communities (Bergfur *et al.* 2009; Layer *et al.* 2010), which in turn influence ecosystem services, such as biomass formation, nutrient cycling, and stability (Gamfeldt & Hillebrand 2008; Goudard & Loreau 2008).

One of the most prevalent anthropogenic stressors of freshwater ecosystems is eutrophication, or extreme increases in primary productivity (Dodds 2007; Smith & Schindler 2009). Stream eutrophication is frequently associated with conversion to agricultural land-use, due to nutrient enrichment from fertilizer or animal run-off and removal of streamside vegetation, which increases temperature and light availability for photosynthesis (Quinn 2000; Hagen *et al.* 2010). Land-use intensification and associated eutrophication of nearby waterways is a global issue, and requires careful management to protect ecosystem health and services (Matson *et al.* 1997; Allgeier *et al.* 2011). Eutrophication alters the form and amount of energy available to food webs; for example, nutrient enrichment stimulates algal growth (Dodds 2007), which in turn influences community composition and energy flow throughout the web (Chapter Two).

Stream food webs typically rely on a mixture of in-stream (autochthonous) and externally-produced (allochthonous) food resources (Cummins 1975). As streams become more eutrophic, the total amount of available energy increases, but the balance of resource availability shifts from allochthonous-dominated to autochthonous-dominated (Hagen *et al.* 2010), which has subsequent impacts on the composition of invertebrate communities and ultimately food-web structure (Finlay 2001). Separating consumers within the aquatic food web into functional feeding groups based on their ability to take advantage of different resources and tracking their responses will provide valuable insights into the mechanisms through which eutrophication affects stream communities (Cummins & Klug 1979; Winterbourn *et al.* 1984). Functional groups are determined by diet and mouthpart morphology (Cummins & Klug 1979; Winterbourn *et al.* 1984). Grazers, also known as scrapers, feed on algal (and bacterial) biofilms scraped off of rocks or other substrates. Shredders primarily consume allochthonous material such as terrestrial leaves and wood when it is available. Collector-browsers consume both algal and detrital matter on the stream bed, while filter feeders capture particles from the water column. Predators feed on other macroinvertebrates. Understanding how increased productivity affects the consumption of autochthonous and allochthonous resources by these functional groups, and the resulting impact on food web structure, will help guide management of ecosystems, especially stream communities, affected by eutrophication.

A shift in the relative availability of basal resources can affect food webs in two ways. Community composition may shift to be dominated by specialist consumers suited to maximize consumption of the more abundant resource (Rasmussen 2010, Chapter Two). As a result, trophic diversity, (*i.e.*, number of occupied niches) may initially increase with expanding autochthonous resources due to increased prevalence of herbivores. These changes may in turn benefit higher trophic levels;

it has been reported that food chain length can increase with ecosystem productivity (Townsend *et al.* 1998). However, as streams become eutrophic, autochthonous production and herbivores may come to dominate, with trophic diversity declining due to the loss of detritivores. Such shifts in community composition, from detrivores to herbivores, are frequently seen along gradients of deforestation (Benstead & Pringle 2004; Gothe *et al.* 2009). Under this scenario, food-web structure and trophic diversity would also likely vary unimodally across a eutrophication gradient, reflecting the diversification and subsequent re-homogenization of resources.

Alternatively, as basal resources shift, organisms may adjust their individual resource use to feed on the more abundant resource (Finlay 2001). This type of response to eutrophication may be prevalent in food webs dominated by generalist species, such as collector-browsers and facultative detritivores, and predators that integrate basal resources by feeding on a wide variety of consumers (Vander Zanden & Vadeboncoeur 2002). In this situation the relative contribution of autochthonous resources to the food web would increase with productivity, but would vary among functional feeding groups.

Understanding the pathways by which environmental-change affects food-web structure will be very useful in designing sustainable long-term management strategies. Furthermore, communities affected by eutrophication may be more susceptible to additional impacts, such as climate change, invasions, or other stressors (Kominoski & Rosemond 2012). The effects of simultaneous multiple stressors often differ from the effects of each individual stressor alone, and the addition of a new stressor can exacerbate existing impacts (Matthaei *et al.* 2010). Determining whether food webs shift in composition or individual consumption, or both, with changes in resource availability will enable more targeted and effective management, such as enhancing resource diversity to mitigate species losses associated with compositional shifts, or attempting to increase colonisation by resource specialists. Predicting and identifying potential effects of eutrophication on stream food webs will also help managers maintain ecosystem functioning and stability, both of which are strongly influenced by food-web structure (Olesen *et al.* 2010; Woodward *et al.* 2012).

The aim of our study was to evaluate the food web-level responses of stream communities to eutrophication. We used stable isotopes to track the changes in resource use by consumers; stable isotopes are a useful tool to study energy transfer and food web structure in ecosystems due to the natural variation in dietary (δ13C) and trophic (δ15N) isotope signatures between consumers and sources (Peterson & Fry 1987). N-signatures become enriched between predator and prey, thus indicating trophic position, while δ13C fractionates little between trophic transfers and can therefore be used to determine ultimate source of carbon (Peterson & Fry 1987; Vander Zanden *et al.* 1999; Post 2002a). We hypothesized that trophic diversity would vary unimodally across a productivity gradient due to increased prevalence of herbivores followed by a subsequent the loss of detritivores. We tested this hypothesis using metrics developed by Layman *et al.* (2007), which use the relative position of species in isotopic biplot space to quantify aspects of trophic structure. Our predicted trends for the individual isotope metrics, which are detailed in the methods, are listed in Table 3.1. Alternatively, we hypothesized that consumers may shift their diets in response to changing resource availabilities, resulting in a change in resource use among species rather than in a change in dominance of feeding groups. We tested this alternate hypothesis by assessing the flow of carbon from basal resources throughout the food web with an isotope mixing model.

Table 3.1: Predicted changes in isotopic food web metrics and potential mechanisms of change across a productivity gradient. Listed below each metric is the food web characteristic which the metric represents.

Metric	Predicted trend with increasing productivity	Potential mechanism
Carbon-range -resource diversity	Initial increase followed by decrease (unimodal relationship)	At low productivity, eutrophication will enhance algal growth, increasing resource diversity. However, highly eutrophic sites are dominated by autotrophic production, which reduces diversity.
Nitrogen-range -food chain length	Linear increase	The increase in autochthonous resources will provide more resources/energy to the food web and thus support more trophic levels.
Trophic Area -trophic diversity	Initial increase followed by decrease (unimodal relationship)	An increase in algal resources will support additional herbivore taxa, but the subsequent decline in allochthonous resources will be associated with the loss of detritivores.
Centroid Distance -average trophic diversity	Initial increase followed by decrease (unimodal relationship)	Same as trophic area.
Mean Nearest Neighbour Distance (MNND) -density of species packing (trophic redundancy)	Initial increase followed by decrease (unimodal relationship)	As resources and taxa become more diverse, MNND will increase (high MNND = less redundant). As resources become more homogenous again at high productivity, taxa diversity and MNND will decline and trophic redundancy will increase.
Standard Deviation Nearest Neighbour Distance (SDNND) -evenness of species packing	Initial decrease followed by increase (u-shaped relationship)	SDNND distance will decline (increasing evenness) with increasing diversity, and later increase (become less even) with increasing homogeneity.

Methods

The study was conducted in the Canterbury region of South Island, New Zealand, an area which has undergone extensive agricultural development since colonization by Polynesian (13th century) and European (late 19th century) settlers (MacLeod & Moller 2006). Development has increased substantially in the last decade, largely due to the intensification of dairy farming (MacLeod & Moller 2006; Pawson & Holland 2008). Eighteen sites were selected among three sub-regions: the Canterbury Plains, Banks Peninsula, and Canterbury foothills (see Chapter Two for details). Each region has a similar range of land use and riparian coverage, ensuring the productivity gradient was not an artifact of regional differences (verified via Mantel test; see Appendix A). Streams were selected along gradients of catchment agricultural land-use intensity and riparian cover (*i.e.* shade), thereby spanning a large gradient of productivity. All streams were of similar size: first or second order and two to three metres wide. Because recent research has shown that high levels of fine sediment have deleterious effects on stream communities (Burdon *et al.* 2013), only streams with primarily cobble substrate were included in the study.

Streams were sampled in late austral summer (February to April) 2010. Reach lengths ranged from 70 to 270 metres, and were scaled to width and discharge. Stream width and depth were measured at ten equidistant points across eight equally-spaced transects along the stream reach; stream velocity was measured both upstream and downstream with a Marsh-McBirney Flo-Mate (Marsh-McBirney, Frederick, Maryland, USA) and stream discharge calculated using standard velocity integration (Gore 2007).

Productivity gradient

A suite of variables related to ecosystem productivity were measured at each site, including: gross primary productivity (GPP), a measure of community metabolism; algal standing stock; shade/riparian cover; and within-stream macrophyte cover. Gross primary productivity was calculated using production and respiration rates for each stream, which were measured using the one-station diurnal oxygen curve technique with propane evasion (Bott 2007; Burrell *et al.* in press). Oxygen concentrations were measured for a span of $2 - 5$ days at each site using D-Opto loggers (Zebratech, Nelson, New Zealand). To minimize variation in photosynthetic production due to cloud cover, loggers were not collected until there had been at least one clear day in the logging period.

Algal biomass was calculated from chlorophyll-*a* concentrations in the biofilm of five large (fist-sized) cobbles collected at random intervals longitudinally within the stream reach. Chlorophyll-*a* was extracted from each cobble in 78˚C ethanol (Sartory & Grobbelaar 1984) and chlorophyll-*a* concentrations measured via fluorometry (Trilogy Laboratory Fluorometer, Turner Designs, Sunnyvale, California, USA). Algal biomass was determined by multiplying the chlorophyll-*a* concentration by the surface area of each rock, which was estimated from three axis measurements (Graham *et al.* 1988). Macrophyte presence/absence and type (submerged or emergent) were recorded at ten points along each transect; these measurements were later summed to obtain percent macrophyte cover for the entire stream reach. Shade measurements were taken at the midpoint of each transect using a densiometer.

Stable isotope sampling and analysis

Macroinvertebrates were collected with a kicknet (500 μm mesh) along the full length of the stream reach with emphasis on sampling all habitat types (riffles, pools, macrophyte beds, overhanging vegetation). Previous quantitative sampling of the eighteen streams (Chapter Two) was used to identify the macroinvertebrate taxa which made up more than 5% of the total abundance in each stream, and a subset of 21 of those taxa which were common across sites were included in the stable isotope analysis (listed in Table 3.2). The samples were frozen and later identified to the lowest practical taxonomic level: genus for mayflies, caddisflies, stoneflies, and snails; subfamily for flies and beetles; subclass for worms; and order (cladocera, amphipods), class (ostracods) or subclass (copepods) for microcrustacea; using (Winterbourn *et al.* 2006) and unpublished keys (B. Smith, NIWA, Hamilton, New Zealand). Snail and caddisfly cases were removed to avoid contamination by non-dietary sources of carbon. Similarly, predator guts were removed to eliminate potential variation in δ15N signatures from ingested organisms (Jardine *et al.* 2005). Macroinvertebrates were oven-dried at 60˚C for at least 48 hours and ground to a fine, homogenous powder with a mortar and pestle. If necessary, multiple individuals of the same taxa were ground together to achieve sufficient biomass for stable isotope analysis. Fish were collected with a backpack electric fishing machine (Kainga 300 EFM, NIWA, Christchurch, New Zealand), identified in the field using McDowall (2001), euthanized with phenoxyethanol, and frozen for later analysis. In the laboratory, samples of dorsal muscle tissue were taken from each fish, oven-dried at 60˚C for at least 48 hours, and ground individually as above.

Algae and terrestrial leaf litter were collected to determine the isotopic composition of basal energy sources. Benthic algae were collected (as described above) as representative autochthonous material. The algal slurry samples were centrifuged at 2500 rpm for 5 min (Labofuge GL, Heraeus-Christ, Osterode, Germany) to coalesce the algal material and then freeze-dried (SuperModulyo 230, Thermo Scientific, Waltham, Massachusetts, USA) for 48 hours to remove all moisture. Submerged leaves were collected from within each stream to represent allochthonous detritus (Finlay 2001) and frozen. Leaf samples were later thawed in the laboratory, rinsed to remove soil and invertebrates, oven-dried at 60˚C for at least 48 hours, and ground in a ball-mill (Mixing Mill 2000, Retsch, Haan, Germany). Leaf type was not distinguished, and multiple leaves from each site were ground together to yield a conglomerate sample.

Samples of ground material (1 mg for invertebrates and fish, 3 mg for algae and leaves) were packed into tins and analyzed at the University of California Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Isotope ratios are reported in delta (δ) notation, defined as the deviation in parts per thousand (‰) from a standard reference material:

$$\delta X = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000,$$

with X representing δ13C or δ15N and R the ratio of 13C/12C or 15N/14N. The standard references were Vienna PeeDee Belemnite limestone for carbon and atmospheric N_2 for nitrogen. The precision of the isotope analysis of our samples was 0.08‰ for δ13C and 0.20‰ for δ15N,

based on the standard deviation of replicates of laboratory standards. Carbon signatures were post-corrected for lipid effects following the mathematical formulas of Post *et al.* (2007) prior to data analysis.

Food web metrics

Six food-web metrics were calculated from the distribution of consumers in isotopic space following the methods of Layman *et al.* (2007), where each node, or consumer, in the food web is represented as a (δ13C, δ15N) point on an isotope biplot. The six metrics were: nitrogen range (NR), carbon range (CR), total area (TA), mean distance to centroid (CD), mean nearest neighbour distance (MNND), and standard deviation of nearest neighbour distance (SDNND). Nitrogen range is the distance between the taxa with the maximum δ15N and the taxa with the minimum δ15N. The NR indicates the vertical structure within a food web, or food chain length and reveals information about the trophic height of the food web. Similarly, carbon range is the distance between maximum and minimum δ13C, and represents the degree of basal resource heterogeneity. Total area (TA) is calculated as the convex hull area of the smallest possible polygon encompassing all points in the δ13C–δ15N biplot space. TA is a surrogate for the total trophic diversity within a food web. Mean distance to centroid is the average distance of each taxa to a centroid located at the mean δ13C and δ15N values for all taxa in the food web, and represents the average degree of trophic diversity. The two nearest neighbour distance metrics describe the relative position of taxa within the biplot space, which indicates trophic niche distribution (Layman *et al.* 2007). Mean NND and standard deviation NND measure the overall density of and evenness of niche packing, respectively. All metrics were calculated in R (R Development Core Team 2011) using the 'SIAR' package (Parnell & Jackson 2011).

Isotope mixing model

We used a mixing model to determine consumer diets. Initially, a *t*-test was performed to confirm that the δ13C signatures of algae (mean δ13C= -33) and leaves (mean δ13C= -28), the two predominant basal resources in stream ecosystems, were statistically distinct ($t = -7.96$, $df = 32.40$, $P < 0.0001$). We then used the stable isotope signatures of basal resources and consumers to fit a Bayesian model (based upon a Gaussian likelihood with a dirichlet prior mixture on the mean) to consumer dietary habits with the 'SIAR' package in R (Parnell & Jackson 2011; R Development Core Team 2011). Trophic fractionation values for the model were calculated from the raw data using the equations of Caut *et al.* (2009). The Bayesian model was chosen because it is based on both δ13C and δ15N, incorporates variation in the input parameters as well as external variation, allows for multiple dietary sources, and generates unique solutions as probability distributions (Parnell *et al.* 2010). The model outputs percent carbon contribution to diet by each source for every consumer. All trophic levels were included in the analysis to test the effectiveness of the mixing model in detecting changes in resource use along the food chain.

Gut contents analysis

Because stable isotope signatures are an integration of multiple sources, it can be difficult to identify the exact prey of predators which may be feeding on a wide range of taxa with isotopic methods (Post 2002a). Furthermore, the mixing model only indicates ultimate basal source (algal or terrestrial carbon), which may or may not allow inference of primary consumer prey type. Therefore the diets of predatory invertebrates and fish were verified via gut contents analysis. The guts of invertebrate predators and fish were removed under a stereomicroscope ($10-63X$ magnification; Nikon SMZ800, Melville, New York, USA) and the contents identified to the lowest possible taxonomic level (genus for mayflies, caddisflies, and snails, family for flies, and class for microcrustacea) and counted. Although gut contents were identifiable, most prey items had been partially digested and/or broken into small fragments, which made volumetric analysis impractical. Consequently gut contents analysis was conducted based on the number of individuals and relative proportion of various prey types consumed by each fish species at a site.

Statistical analysis

A principal components analysis (PCA) was conducted on the multiple productivity measures to create a single composite productivity axis, which will hereafter be referred to as the "productivity gradient." The environmental variables included in the PCA analysis were shade, macrophyte cover, particle size, nutrients (nitrate and ammonium), chlorophyll-a, productivity (GPP), heterotrophic respiration, and particulate organic matter (POM). Variables were log-transformed when necessary to meet assumptions of normality. The PCA was run in R using the 'prcomp' function; variables were scaled to have unit variance through division by the root mean square prior to analysis. Variables with PCA loadings > 0.7 were considered significant environmental factors contributing to the gradient.

Linear regression was used to test for shifts in basal carbon use with increasing productivity. The mean percent of algal consumption calculated by the mixing model for each invertebrate functional feeding group and fish species within a site was regressed against the PCA productivity gradient. Homogeneity of slopes tests were performed to evaluate differences in feeding group-productivity relationships. To assess the efficacy of the mixing model for higher trophic levels, we also performed gut content analyses on predatory invertebrates and fish. Predator dietary preferences were calculated as the log-ratio of prey abundance in predator guts to relative prey abundance at the site (based on Chesson (1978)). Lastly, we investigated whether food-web structure changed in response to shifts in basal resource consumption and prey preference by testing the six food web metrics individually against the productivity gradient with linear regression. Variables were arcsine-square-root- (percent algal contribution) or log- (Layman metrics) transformed if necessary to meet assumptions of normality prior to analysis. All statistical analyses were carried out using R (R Development Core Team 2011).

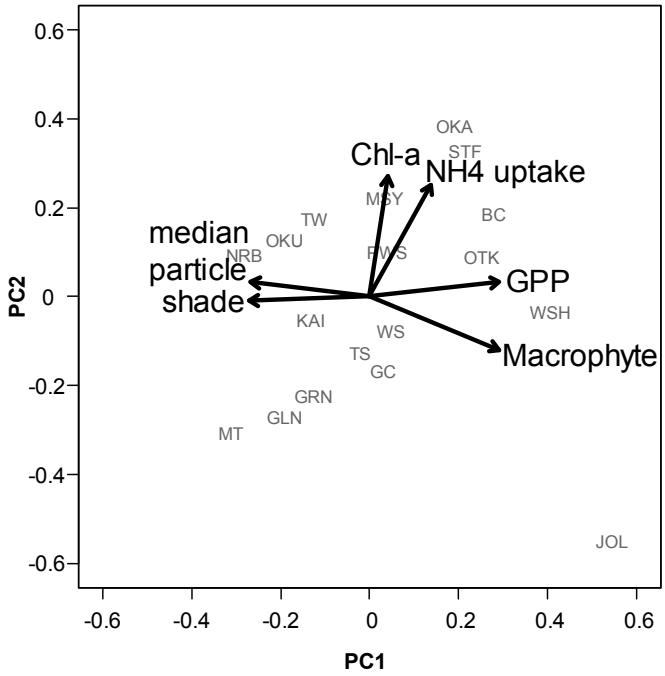

Figure 3.1: Principal components analysis (PCA) of environmental variables across 18 streams in the Canterbury region, South Island, New Zealand. Each PCA axis represents an environmental gradient, and arrows show variables with axis loadings > 0.7, indicating environmental variables (see Methods section in the text for details) associated with each axis. The direction of the arrow denotes the direction of correlation, and text in capital letters indicate individual streams (abbreviations listed in Table 3.2).

Results

The principal components analysis indicated that gross primary productivity, macrophyte cover, and shade were responsible for the majority of the variation in productivity. These variables were all associated with the first PCA axis, which explained 44% of the total variance in environmental factors included in the analysis (Figure 3.1). Low productivity sites were characterized by shade, while highly productive sites had increased macrophyte coverage and high GPP (Chapter Two).

Food-web structure, as determined from the isotope metrics, varied across the productivity gradient. For example, a food web from a low-productivity stream was smaller and the consumer points were closer together, whereas a high-productivity stream had a larger food web with a greater range of isotope signatures (Figure 3.2). Isotopic metrics for each stream food web are listed in Table 3.2. Contrary to our prediction, the relationships between food web characteristics and productivity were not unimodal hump-shaped curves (Figure 3.3). The C-range, a proxy for resource heterogeneity, did not peak at intermediate productivity as we expected, but increased continuously over the productivity gradient ($F_{1,16} = 10.86$, $P < 0.01$, $R^2 = 0.40$). The N-range did not change over the gradient ($F_{1,16} = 0.034$, $P > 0.10$, $R^2 = 0.002$). Trophic area, or total trophic diversity, was significantly correlated with the productivity gradient ($F_{1,15} = 19.27$, $P < 0.001$, $R^2 = 0.53$) when one potential outlier was removed (outlier not removed: $F_{1,16} = 2.32$, $P > 0.10$, $R^2 = 0.13$), indicating that food webs expanded in isotopic space (*i.e.* increased trophic diver-

sity) with increasing productivity. Similarly, centroid distance also had a positive relationship with productivity ($F_{1,16} = 6.23$, $P < 0.05$, $R^2 = 0.28$), indicating that the average, as well as total, trophic diversity of food webs increased with productivity. Mean nearest neighbour distance ($F_{1,16} = 12.16$, $P < 0.01$, $R^2 = 0.43$) also had a positive correlation with productivity, showing that the density of niche packing, or trophic redundancy, declined in high productivity sites. However, there was no significant relationship between standard deviation of the nearest neighbour distance and productivity ($F_{1,16} = 3.59$, $P > 0.05$, $R^2 = 0.18$), indicating that the evenness of niche packing was unchanged across the gradient. In summary, as productivity increased, food webs expanded horizontally but not vertically, and had greater trophic diversity but less dense niche packing and reduced trophic redundancy.

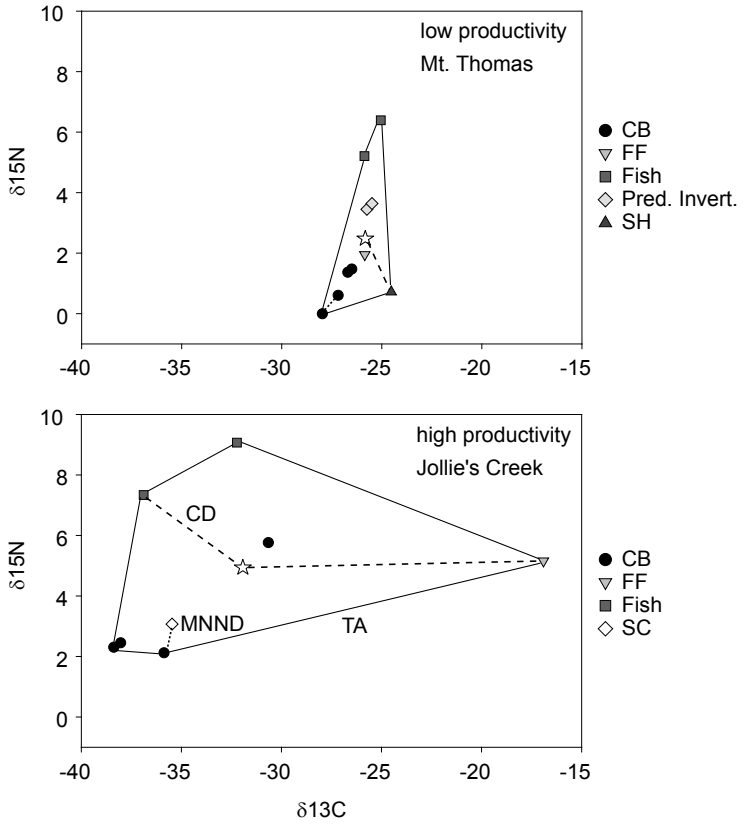

Figure 3.2: Representative isotope biplots of food webs in low productivity (Mt. Thomas) and high productivity (Jollie's Creek) streams. Points represent different functional feeding groups: CB – collector-browsers; FF – filter feeders; Fish – fish; Pred. Invert. – predatory invertebrates; SH – shredders; and SC – scrapers. Examples of the measurements used to derive the isotopic metrics are also shown: solid lines indicate total area (TA), the polygon formed by connecting the outermost points in all directions; dashed lines indicate centroid distance (CD), the distance between each point and the polygon centroid, shown as a star on the plot; and dotted lines indicate mean nearest neighbour distance (MNND), the distance between each point and the point closest to it.

Our second hypothesis, that resource use by different functional groups of invertebrates would shift with increasing productivity, was supported by the mixing model. The mixing model indicated that all functional groups except predatory invertebrates significantly increased in mean

percent algal composition, indicating increased autochthonous carbon consumption with increasing productivity (Figure 3.4). The rate of increase, or slopes of the percent algal contribution-productivity regressions, differed significantly between functional groups (percent algal contribution-functional group interaction: $F_{5,132} = 2.55$, $P < 0.05$). Facultative shredders increased in percent algal composition the most, from 10 percent in low productivity sites to 97 percent in the highest productivity site ($F_{1,5} = 12.47$, $P < 0.05$, $R^2 = 0.71$), indicating a switch from reliance on allochthonous to almost total consumption of autochthonous carbon. Collector-browsers and filter feeders increased in relative algal contribution by 74 and 78 percent, respectively, over the productivity gradient (collector-browsers: $F_{1,16} = 24.08$, $P < 0.001$, $R^2 = 0.60$; filter feeders: $F_{1,14} = 12.90$, $P < 0.01$, $R^2 = 0.48$). Scrapers had the highest algal contribution of all invertebrate groups (28 percent) in the lowest productivity site, and increased 58 percent across the gradient ($F_{1,10} = 13.30$, $P < 0.01$, $R^2 = 0.57$). However, converse to our expectation, predatory invertebrate signatures only weakly reflected the changing algal consumption of primary consumers ($F_{1,14} = 3.91$, $P = 0.07$, $R^2 = 0.22$).

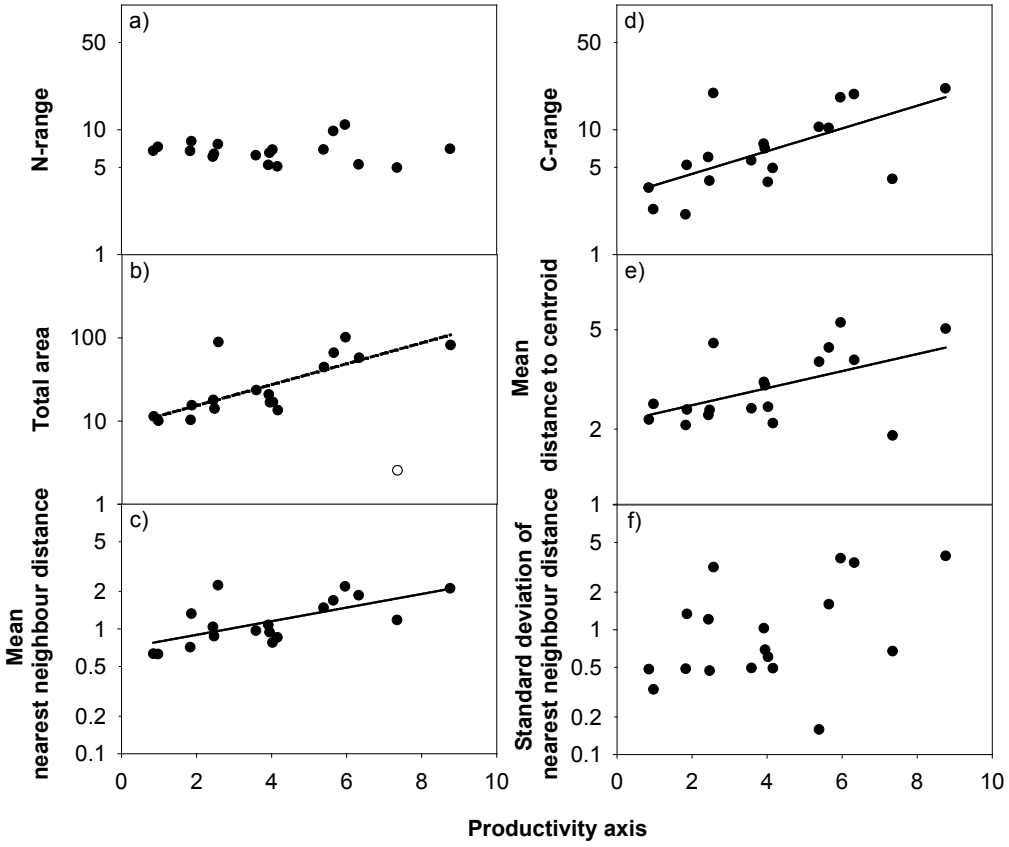

Figure 3.3: Linear regressions of isotopic food web metrics along the productivity gradient in 18 lowland Canterbury Plains streams. The productivity axis is the first axis from the productivity PCA (Figure 3.1). The isotopic metrics include: a) N-range, b) total area (TA), c) mean nearest neighbour distance (MNND), d) C-range, e) mean distance to centroid (CD), and f) standard deviation of nearest neighbour distance (SDNND). Further details about each metric are given in the methods section of the text. All metrics were log-transformed prior to analysis. Each point is a site, indicating the value of the metric for the food web in that stream. Solid lines indicate significant relationships at $P < 0.05$. The dashed line in plot b) indicates the significant relationship between TA and productivity when a potential outlier (open circle) is removed.

Table 3.2: Productivity (PCA axis score), isotopic metric value (calculated from the stable isotope biplots for each food web), and taxa included in stable isotope analysis for each stream. The functional feeding group classification for each taxa is listed in brackets following the taxa name. Functional feeding groups include: collector-browsers (CB), filter feeders (FF), facultative shredders (SH), scrapers (SC), predatory invertebrates (PI), and fish (PF). Site abbreviations are also given below each site name.

Site	Productivity (PCA score)	Food Web Isotope Metric						Taxa Sampled
		N-range	C-range	Total Area	Centroid Distance	MNND	SDNND	
Boggy Creek (BC)	6.32	5.28	19.31	57.71	3.79	1.86	3.45	Conoesucidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), Ostracoda (FF), *Potamopyrgus* (SC), Elmidae (SH), Brown Trout (PF), Common Bully (PF), Longfin Eel (PF), Shortfin Eel (PF)
Gammans Creek (GC)	4.02	6.93	3.82	16.92	2.46	0.78	0.61	Chironomidae (CB), Cladocera (CB), Conoesucidae (CB), *Deleatidium* (CB), Oligochaeta (CB), *Hydropsyche* (FF), Ostracoda (FF), *Potamopyrgus* (SC), Elmidae (SH), *Archichauliodes* (PI), Hydrobiosidae (PI), *Stenoperla* (PI), Canterbury Galaxias (PF),Upland Bully (PF)
Glentui (GLN)	1.86	8.09	5.22	15.5	2.4	1.33	1.34	Conoesucidae (CB), *Deleatidium* (CB), *Helicopsyche* (CB), *Zelandobius* (CB), *Hydropsyche* (FF), Elmidae (SH), *Archichauliodes* (PI), Hydrobiosidae (PI), *Stenoperla* (PI)

Site	Productivity (PCA score)	Food Web Isotope Metric						Taxa Sampled
		N-range	C-range	Total Area	Centroid Distance	MNND	SDNND	
Grehan (GRN)	2.43	6.09	6.05	17.94	2.28	1.04	1.21	Conoesucidae (CB), *Helicopsyche* (CB), *Hydropsyche* (FF), *Potamopyrgus* (SC), *Archichauliodes* (PI), Hydrobiosidae (PI), Longfin Eel (PF), Giant Bully (PF), Upland Bully (PF)
Jollie's Creek (JOL)	8.76	7.04	21.47	82.13	5.06	2.12	3.91	Amphipoda (CB), Conoesucidae (CB), Cladocera (CB), *Deleatidium* (CB), Ostracoda (FF), *Potamopyrgus* (SC), Brown Trout (PF), Upland Bully (PF)
Kaituna (KAI)	2.47	6.41	3.91	14.14	2.39	0.88	0.47	Conoesucidae (CB), Chironomidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), *Potamopyrgus* (SC), *Archichauliodes* (PI), Hydrobiosidae (PI), Brown Trout (PF), Longfin Eel (PF), Upland Bully (PF)
Mounseys (MSY)	3.91	5.23	7.73	20.91	3.09	1.08	1.03	Conoesucidae (CB), Cladocera (CB), *Deleatidium* (CB), *Potamopyrgus* (SC), Hydrobiosidae (PI), Canterbury Galaxias (PF), Upland Bully (PF)
Mt. Thomas (MT)	0.85	6.8	3.44	11.39	2.19	0.63	0.48	Conoesucidae (CB), Chironomidae (CB), *Deleatidium* (CB), *Zelandoperla* (CB), *Hydropsyche* (FF), Elmidae (SH), *Archichauliodes* (PI), *Stenoperla* (PI), Brown Trout (PF), Longfin Eel (PF)

Site	Productivity (PCA score)	Food Web Isotope Metric						Taxa Sampled
		N-range	C-range	Total Area	Centroid Distance	MNND	SDNND	
Narby (NRB)	0.97	7.3	2.31	10.09	2.52	0.63	0.33	Conoesucidae (CB), Chironomidae (CB), *Deleatidium* (CB), *Zelandoperla* (CB), *Hydropsyche* (FF), *Potamopyrgus* (SC), Elmidae (SH), *Archichauliodes* (PI), Hydrobiosidae (PI), Bluegill Bully (PF), Canterbury Galaxias (PF), Giant Bully (PF), Longfin Eel (PF), Redfin Bully (PF), Torrentfish (PF)
Okana (OKA)	5.38	6.95	10.55	44.59	3.73	1.48	0.16	Conoesucidae (CB), *Deleatidium* (CB), *Oxyethira* (CB), Ostracoda (FF), *Potamopyrgus* (SC), Hydrobiosidae (PI), Brown Trout (PF), Giant Bully (PF), Inanga (PF), Shortfin Eel (PF), Upland Bully (PF)
Okuti (OKU)	1.83	6.77	2.1	10.34	2.08	0.71	0.49	Conoesucidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), *Potamopyrgus* (SC), *Archichauliodes* (PI), Hydrobiosidae (PI), Tanypodinae (PI), Brown Trout (PF), Longfin Eel (PF), Upland Bully (PF)
Otukaikino (OTK)	5.96	10.99	18.19	101.85	5.35	2.19	3.75	Conoesucidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), Ostracoda (FF), *Potamopyrgus* (SC), Hydrobiosidae (PI), Longfin Eel (PF), Upland Bully (PF)

Site	Productivity (PCA score)	Food Web Isotope Metric						Taxa Sampled
		N-range	C-range	Total Area	Centroid Distance	MNND	SDNND	
Pawsons (PWS)	3.94	6.54	7.1	16.78	3	0.94	0.69	Conoesucidae (CB), *Deleatidium* (CB), *Zelandoperla* (CB), *Hydropsyche* (FF), *Potamopyrgus* (SC), *Archichauliodes* (PI), Hydrobiosidae (PI), Bluegill Bully (PF), Shortfin Eel (PF)
Steffens (STF)	5.64	9.78	10.36	66.27	4.25	1.69	1.6	Conoesucidae (CB), Chironomidae (CB), Cladocera (CB), *Deleatidium* (CB), *Hydropsyche* (FF), Ostracoda (FF), *Archichauliodes* (PI), Hydrobiosidae (PI), Shortfin Eel (PF), Upland Bully (PF)
Te Wharau (TW)	2.57	7.67	19.71	89.21	4.42	2.24	3.18	Conoesucidae (CB), *Deleatidium* (CB), *Helicopsyche* (CB), Oligochaeta (CB), Ostracoda (FF), *Potamopyrgus* (SC), *Archichauliodes* (PI), Hydrobiosidae (PI), Bluegill Bully (PF), Lamprey (PF), Longfin Eel (PF)
Trout Stream (TS)	3.58	6.25	5.69	23.57	2.42	0.97	0.49	Conoesucidae (CB), Chironomidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), *Austrosimulium* (FF), Elmidae (SH), *Archichauliodes* (PI), Hydrobiosidae (PI), *Stenoperla* (PI), Canterbury Galaxias (PF), Upland Bully (PF)

Site	Productivity (PCA score)	Food Web Isotope Metric						Taxa Sampled
		N-range	C-range	Total Area	Centroid Distance	MNND	SDNND	
Washpool (WSH)	7.34	4.98	4.04	2.55	1.89	1.18	0.67	*Deleatidium* (CB), *Potamopyrgus* (SC), Hydrobiosidae (PI), *Xanthocnemis* (PI), Common Bully (PF)
White Stream (WS)	4.15	5.09	4.94	13.53	2.11	0.86	0.49	Conoesucidae (CB), *Deleatidium* (CB), *Hydropsyche* (FF), *Austrosimulium* (FF), Elmidae (SH), *Archichauliodes* (PI), Hydrobiosidae (PI), Canterbury Galaxias (PF), Upland Bully (PF)

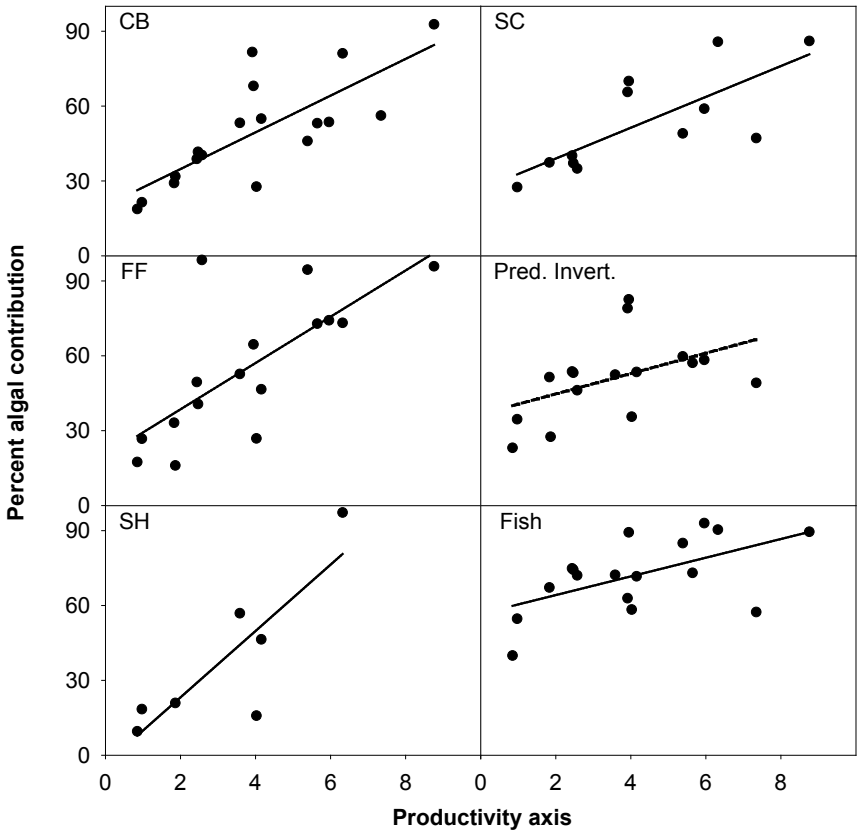

Figure 3.4: Percent algal composition of functional feeding groups across the productivity gradient in 18 lowland Canterbury Plains streams. The productivity axis is the first axis from the productivity PCA (Figure 3.1). Feeding groups include: collector-browsers (CB), filter feeders (FF), facultative shredders (SH), scrapers (SC), predatory invertebrates (Pred. Inverts.), and fish. Each point represents the mean percent algal composition of all members of a feeding group within a site. Solid lines indicate signficant relationships at $P < 0.05$, whereas dashed lines indicate $0.05 < P < 0.1$.

Fish changed significantly in their incorporation of algal-derived energy across the productivity gradient, indicating that the change in carbon source was being passed up the food web. Fish had higher algal contributions (40 percent) than any of the invertebrate groups at low productivity, but only increased by 50 percent across the productivity gradient ($F_{1,15} = 7.63$, $P < 0.05$, $R^2 = 0.34$), compared to an average 74 percent increase by invertebrate primary consumers (excluding predatory invertebrates) across the productivity gradient. However, there was considerable variation between fish taxa (Figure 3.5). Although a homogeneity of slopes test among fish species was not significant ($F_{3,22} = 2.67$, $P > 0.05$), there was a difference in slopes of the productivity-algal contribution relationships between large and small fish (percent algal contribution:size interaction $F_{1,26} = 4.16$, $P = 0.05$). Larger fish had significant positive relationships between algal composition and productivity (brown trout: $F_{1,4} = 29.61$, $P < 0.01$, $R^2 = 0.88$; longfin eel: $F_{1,6} = 25.47$, $P < 0.01$, $R^2 = 0.81$), while the smaller fish did not (Canterbury galaxias: $F_{1,3} = 0.05$, $P > 0.10$, $R^2 = 0.02$; upland bully: $F_{1,9} = 4.39$, $P > 0.05$, $R^2 = 0.33$). Moreover, the galaxiids and upland bullies both had high algal contribution at low levels of productivity (60 and 69 percent) and increased less than 20 percent across the gradient, whereas brown trout and longfin eels had

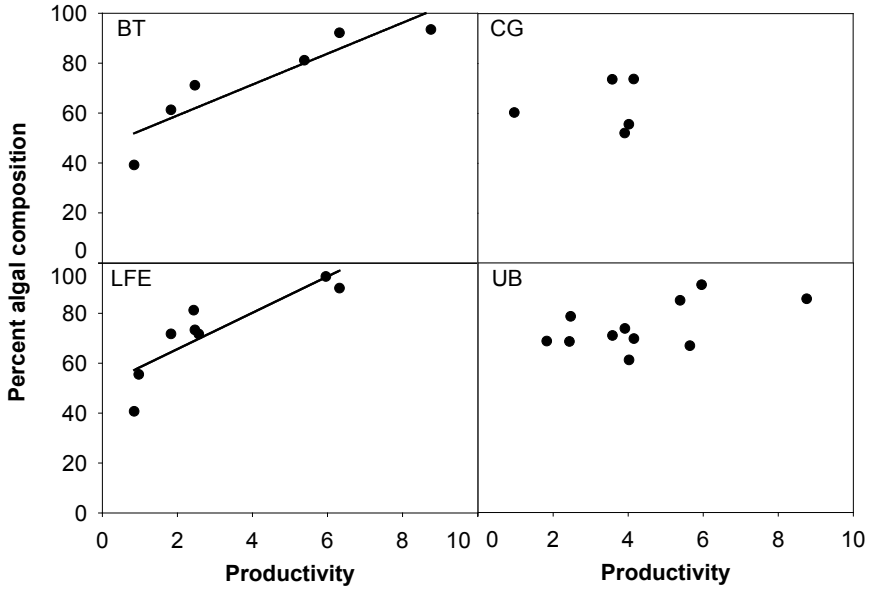

Figure 3.5: Percent algal composition of fish species across the productivity gradient in 18 lowland Canterbury Plains streams. The productivity axis is the first axis from the productivity PCA (Figure 3.1). Fish species include: brown trout (BT), longfin eel (LFE), Canterbury galaxias (CG), and upland bully (UB). Each point represents the mean percent algal composition of all members of that species within a site. Solid lines indicate signficant relationships at $P < 0.05$.

lower algal contributions at low productivity (39 and 41 percent respectively), but approximately doubled those amounts in high productivity streams.

To determine whether the variations in algal composition of fish taxa were influenced by the type of prey consumed, we used gut content analysis to evaluate prey preference between fish species across the productivity gradient (Table 3.3). Fish consumed prey from all feeding groups, although brown trout and longfin eels selected against defended prey such as snails and ostracods (the two smaller species did not discriminate against these taxa). All fish species had strong positive selection on large, soft-bodied prey such as *Deleatidium* mayflies and uncased caddisflies *Hydropsyche* (*Aoteapsyche*-group) and Hydrobiosidae. However, high preference scores were negatively correlated with the productivity gradient (Table 3.3), indicating that preferred prey were less available in high productivity sites.

Table 3.3: Selection scores (mean log ratio) of fish on invertebrate prey, determined from gut contents analysis, and correlation between selection scores and the productivity axis across all sites. The details of the selection calculation are given in the text. *n* is the number of sites (*i.e.* data points) in each correlation.

	upland bully			longfin eel			brown trout			Canterbury galaxias		
prey taxa	Mean log ratio	Correlation	n	Mean log ratio	Correlation	n	Mean log ratio	Correlation	n	Mean log ratio	Correlation	n
Hydropsyche	0.65	-0.25	5	0.96	-0.14	4	1.46		1	1.1		1
Austrosimulium	1.21	-0.5	5	1.43	-0.09	2	1.44		1	0.77	0.31	2
Coloboriscus	2		1	1.45	-0.38	4	0.96		1			0
Conoesucidae	-0.99	0.52	3	-0.32	0.58	6	0.28	0.39	5	0.32	0.37	3
Deleatidium	0.42	-0.42	9	0.91	0.24	6	0.41	-0.09	5	0.16	-0.76	5
Hydrobiosidae	0.75	-0.55	7	1.35	-0.42	4	0.54	-0.72	4	1.2	-0.35	5
Orthocladinae	-0.22	-0.29	7	-0.02		1	-0.98	-0.18	3	-0.06	0.07	3
Ostracoda	0.29	-0.25	8	-1.03		1	-1.03		1	0.79		1
Oxyethira	0.67	0.44	6			0	1.49	0.41	2	0.26		1
Snails	0.39	-0.17	9	-0.03	0.56	4	-0.93	0.01	2			0

Discussion

As human populations continue to grow, there is a pressing need for sustainable management of both land and waterways, particularly with regard to eutrophication, which is an increasing concern worldwide (Allgeier *et al.* 2011). Understanding how eutrophication affects stream communities and food-web structure will be critical in developing effective management strategies to maintain ecosystem health and stability. In our study of 18 stream food webs across a productivity gradient, spanning three orders of magnitude of GPP, we found that stream eutrophication was associated with shifts in resource availability and use, which were in turn linked to changes in food web structure. Consumption of autochthonous production by all functional groups increased across the productivity gradient, contradicting a common assumption that aquatic communities respond to changes in resource availability by shifting in functional composition from shredders to grazers (Vannote *et al.* 1980; Rasmussen 2010). Moreover, the increase in autochthonous carbon content was not limited to first-level consumers, but was evident throughout the food web. Surprisingly, however, trophic height, a common measure of food chain length, did not increase with productivity, contrary to theoretical predictions and some previous empirical work (Pimm 1982; Schoener 1989; Townsend *et al.* 1998; Post 2002a). These partially unexpected results shed light on the complex effects of eutrophication on stream food webs, and indicate that resource diversity is potentially as important as total resource quantity. We found that differential responses of functional feeding groups to increasing autochthonous resources alter food web structure, which in turn mediates the effect of productivity on food chains.

Our hypothesis that food webs would become primarily autochthonously-based with increasing eutrophication was supported by our isotope mixing models, but the food web metrics did not mirror the changes in resource diversity as we predicted. We hypothesized that trophic diversity would increase with greater resource diversity, and then decline again as autochthonous resources became more abundant, forming a unimodal curve. Thus the highest trophic diversity would occur at mid-productivity when both detrital and algal pathways were present. Instead, trophic diversity increased linearly across the productivity gradient because all taxa increased their relative consumption of autochthonous resources, suggesting invertebrate communities were largely composed of trophic generalists at all productivity levels. Therefore there was no shift from specialist detrivores to specialist herbivores with productivity.

True food specialists are actually rare in New Zealand, where most stream invertebrates are opportunists which feed on a wide variety of foods and have adaptive diets (Lester *et al.* 1995; Winterbourn 2000). For example, Rounick *et al.* (1982), investigating the effects of deforestation on stream communities, reported small changes in community composition but increased dependence on autochthonous resources by multiple taxa with a variety of feeding modes. Furthermore, such results are not unique to New Zealand. Both a study on natural gradients of stream resources in the southeastern United States (Rosi-Marshall & Wallace 2002) and a comparison between clear-cut and forested streams in Sweden (Gothe *et al.* 2009) documented diet changes across functional feeding groups in conjunction with changes in resource availability. The lack of any unimodal productivity-trophic diversity relationship across our study streams similarly suggests that consumers are responding to changes in productivity (*i.e.* resource availability) by

switching diet, explaining why we did not observe increased specialization at either end of the autochthonous-allochthonous resource gradient.

These changes in diet were also associated with substantial shifts in food-web structure. All feeding groups increased their consumption of algal-derived carbon, but began to switch at different points along the productivity gradient, indicated by the difference in slope of the percent algal contribution-productivity gradient relationships between functional feeding groups; some rapidly increased in algal carbon content with increasing productivity while others remained more reliant on terrestrial carbon. These variations in turn drove the observed changes in overall food web structure: because diets changed at different rates, the isotopic signatures of taxa diverged and taxa separated in biplot space, increasing trophic diversity (total area and centroid distance) and reducing trophic redundancy (MNND) (3.6). As a result, food webs stretched horizontally with productivity and food-web breadth (*i.e.* C range) increased as generalists broadened their niche width by adjusting their reliance between resources.

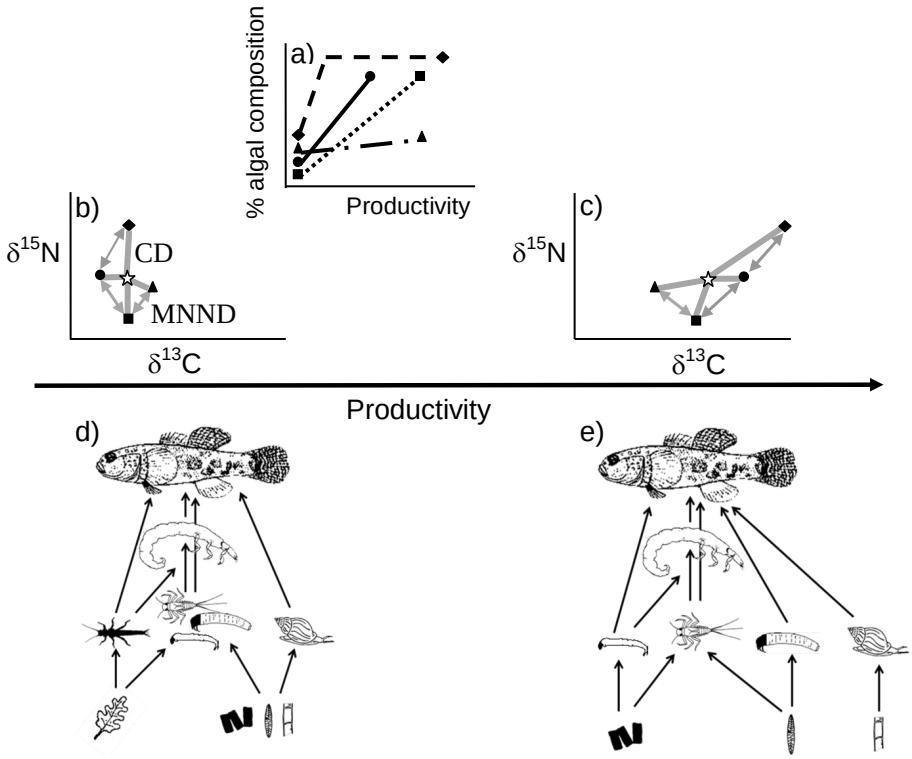

Figure 3.6: Likely changes in food web structure with increasing productivity in Canterbury Plains streams. The upper diagram (a) illustrates variations in timing of diet shifts among functional feeding groups (black symbols, with predators at the top feeding upon primary consumers below and lines indicating trajectories of change) corresponding with the shift for that feeding group in biplot space from low productivity (b) to high productivity (c). On the two biplot graphs (b) and (c) the thin gray double arrows between black symbols indicate mean nearest neighbour distance (MNND), while the thick gray lines between each feeding group (black) symbol and the white star indicate centroid distance (CD); the white star is the centroid, a point located at mean δ13C and δ15N for the entire food web. Diagrams d) and e) show how the shifts in bipolot space translate to changes in food web structure; increasing specialization on a single resource results in increased trophic diversity, but less species diversity, and expands the food web horizontally along the resource (δ13C) axis.

It is important to note, however, that C-range represents the population niche breadth, rather than individual niche breadth, and a larger C-range does not necessarily indicate that individuals within the group are each feeding more generally. Instead, generalists as a group are broadening in niche. In fact, the increases in trophic diversity and reduced trophic redundancy we observed suggest the possibility of finer-scale specialization on algal resources among the generalist herbivores. Several studies have reported such specialization by stream invertebrates via preferential selection of algal particles of various sizes and positions in the biofilm matrix (Parkyn *et al.* 2005; Tall *et al.* 2006a). For example, a gut contents analysis of various stream grazers indicated three distinct feeding modes: one group, which the authors termed "surfers," ate only loose (unattached) overstory diatoms, while a second group, the "true scrapers," avoided the overstory and fed preferentially on attached diatoms lower in the periphyton matrix (Tall *et al.* 2006a). A third group of generalists showed no spatial selection of diatoms. A second study found that grazers also select diatoms as a function of their size, *i.e.* larger grazers (size measured as head width) feed preferentially on larger diatoms (Tall *et al.* 2006b). Additionally, even invertebrates with similar feeding modes and diets can differ in their ability to assimilate algal carbon (Aberle *et al.* 2005). Broekhuizen *et al.* (2002) found that *Deleatidium* mayflies had an assimilation rate six times higher than *Potomopyrgus* snails fed an identical algal diet. Likewise, Parkyn *et al.* (2005) reported differences in both C- and N-isotope assimilation between *Deleatidium*, *Potamopyrgus*, and *Olinga feredayi*, a facultative shreddering caddisfly, fed the same diet in experimental channels. Variations in growth rates and turnover times may also result in differences in uptake and assimilation rates between invertebrate taxa (Hall 1995). Thus, the increases in trophic diversity and C-range we observed could indicate increasing specialization by generalists on different components of the algal matrix, as illustrated in Figure 3.6.

Despite the horizontal expansion of food webs in biplot space along the eutrophication gradient due to increased C-range and increased trophic diversity, vertical food-web structure (i.e. N-range) did not appear to be influenced by changes in productivity. This was surprising, given that energetic theory predicts more productivity should support more trophic levels (Pimm 1982; Schoener 1989), and many studies have reported longer food chain lengths with increasing productivity in aquatic (Sabo *et al.* 2009) and terrestrial (Arim *et al.* 2007; Young *et al.* 2013) ecosystems. However, a comparison of food webs from many different ecosystem types did not find any difference in food chain length between high and low productivity webs (Briand & Cohen 1987) and several subsequent studies in both lakes (Vander Zanden *et al.* 1999; Post *et al.* 2000) and rivers (Jepsen & Winemiller 2002; Sabo *et al.* 2010) similarly found no relationship between productivity and food chain length. Therefore, there is certainly no general relationship between productivity and food chain length. Moreover, Davis *et al.* (2010) reported that long-term nutrient enrichment actually reduced trophic transfer efficiency between predators and prey due to trophic bottlenecks generated by increasing abundances of predation-resistant prey. We also found evidence of trophic bottlenecks in high productivity sites, namely increased relative abundance of defended primary consumers (Chapter Two). These taxa are selected against by fish, according to our dietary analysis as well as previous research on these fish species (McIntosh 2000), suggesting that food chain lengths are not increasing because energy is being trapped in unpalatable defended consumer biomass. Changes in trophic omnivory have also been hypothesised to influence food

chain length (Post & Takimoto 2007). If fish responded to the changes in community composition and prey availability by increasing omnivory, food chain lengths would also decline (Post & Takimoto 2007), as observed in this study. Thus, increases in food chain length may not always result from increased productivity, due to complex food web interactions, especially if they result in trophic bottlenecks.

The lack of increase in food chain length in this study also suggests that the increasing abundance of autochthonous carbon is not enough to compensate for the loss of other energy pathways. In that regard, eutrophication is a unique stress because typically the total amount of available energy increases despite decreases in resource diversity. Therefore, consumers can switch to more abundant energy sources, as we observed, but this may not result in increased trophic height. Furthermore, although trophic diversity increased with productivity due to the divergence of trophic niches/isotope signatures among trophic generalists, species diversity declined across the productivity gradient (Chapter Two). Thus, while increasing specialization of trophic generalists on a single (autochthonous) resource maintains isotopic food-web structure in eutrophic streams, it may also exacerbate declines in species diversity, because generalists, especially those less vulnerable to predation, most likely competitively exclude specialist taxa when their resources become scarce (Huxel *et al.* 2002).

It is also questionable whether ecosystem functions are sustained by trophic generalists when species diversity declines. Although they did not consider dietary shift as a causal mechanism, Woodward *et al.* (2012) reported decreasing rates of invertebrate-mediated leaf litter breakdown with increasing nutrient enrichment. It has also been suggested that the relative contribution of a given taxa to an ecosystem process may shift along an environmental gradient (Wellnitz & Poff 2001), such as productivity. Taxa may be redundant at some points along a gradient but not others (Poff *et al.* 2003). Additionally, not all organisms are equal; some, such as large predators at higher trophic levels, have been found to exert a disproportionate effect on ecosystem function (Woodward 2009). However, even though a single dominant species may provide the bulk of certain functions (Smith & Knapp 2003), higher species richness is still required to provide multiple ecosystem functions (Zavaleta *et al.* 2010). These studies suggest that species diversity, rather than trophic niche diversity, is more important for maintaining ecosystem function. Moreover, recent research indicates that it is the functional traits which vary between species, rather than species identity per se, that determines the effect of biodiversity on ecosystem function (Reiss *et al.* 2009). Thus, while eutrophication enhances trophic diversity, it may still negatively impact ecosystem functions via losses in key functional species or traits.

Similarly, the shifts in resource use by trophic generalists we observed along the productivity gradient may have maintained food web structure, but they did not necessarily maintain food web stability. An ecosystem's ability to withstand perturbation depends on the ability of species to respond differently to the perturbation, thus increasing the chances of there being species present which continue to function under the stress (McCann 2000; Naeem 2002). Food webs with diverse basal resources (Huxel *et al.* 2002), a greater number of energy pathways (MacArthur 1955), and greater numbers of trophic generalists (Woodward 2009) should be more stable, as diffuse networks are buffered against loss of a particular resource or pathway (Woodward 2009). The increased reliance of the entire food web on a single energy pathway, declines in trophic redundancy,

and decreased prey availability for large predators that we observed in high productivity streams suggests that increased eutrophication may have compromised ecosystem stability. These destabilizing forces may be partially balanced by the large proportions of trophic generalists common to eutrophic streams, which have greater capacity to maintain food web structure, and therefore stability, despite resource homogenization (Woodward 2009). Theoretical models indicate that adaptive foraging, or diet switching, can enhance food web flexibility; because only a subset of the potential links are operating at a given time, food webs can rapidly restructure in response to perturbation, thereby enhancing stability (Valdovinos *et al.* 2010). However, increased specialisation within a food web on a single resource may not be dynamically equivalent to generalists switching amongst multiple resources. Further research is required to advance our understanding of the relative influences of species, functional, and trophic diversity on food web structure and stability. For example, do increases in trophic diversity offset the loss of species diversity and maintain stability, or is the loss of species an indication of decreased stability at high productivity, despite increases in trophic diversity?

Overall, our study indicates that eutrophication can have a combination of counter-intuitive influences on ecosystem health, function, and stability. Despite increasing the total available energy, eutrophication impairs ecosystem health, for while the amount of available resources increases, the diversity of resources declines. Trophic generalists maintain food web structure by specializing on different autochthonous components, increasing trophic diversity, but the increased energy does not make it up the food web to higher trophic levels, creating bottlenecks and potentially unstable food webs. Based on our findings, we have identified three key questions for future study: 1) Are resource specialists being excluded by trophic generalists? 2) Does the loss of resource specialists lead to decreased food web stability, or is the new configuration (community of trophic generalists) equivalently stable? 3) Does the new configuration maintain ecosystem function? We suggest that experimentally reintroducing allochthonous resources into eutrophic streams may be one fruitful approach for investigating these questions and further testing the mechanisms controlling food web structure, stability, and ecosystem function. If specialists are being excluded by generalists, increasing detrital resources may retain detritivorous taxa, and reduce the dramatic shifts in diet by generalists, thus enhancing species and/or functional diversity. The relative stability and functional performance of trophically-diverse versus species-diverse webs can be tested experimentally using factorial combinations of specialist and generalist taxa and measuring their resistance and resilience to artificial perturbations (Donohue *et al.* 2013). The results of these experiments will indicate to managers whether they should focus on maintaining functional diversity or trophic diversity in order to sustain ecosystem function and stability, and if restoring resource diversity can mitigate the negative effects of eutrophication on stream communities.

4

Generalist taxa showed greatest response to reintroduction of allochthonous subsidies during restoration of lowland agricultural streams

Abstract

Re-planting riparian vegetation is increasingly promoted as a stream restoration tool worldwide. Riparian restoration improves water quality and in-stream physical habitat, but its effectiveness for improving stream invertebrate communities, particularly with regard to the role of allochthonous organic matter inputs, is relatively untested. We conducted a short-term resource manipulation experiment to test the effects of relative allochthonous resource availability on invertebrate community composition in six degraded, eutrophic, lowland agricultural streams. We added 133 large (250 gram) leaf packs to a 200 metre stream reach in three streams and maintained three control streams that did not receive large leaf packs. Twelve rock baskets within each stream reach received a cross of shading and further basket-level leaf addition treatments. Baskets were incubated in the streams for six weeks to allow invertebrate colonisation, and invertebrate communities were compared using a linear mixed effects analysis. Interactions between reach-scale and basket-scale manipulations had strong influences on invertebrate community composition. Shifts in invertebrate richness and evenness were largely driven by increased dominance of generalist taxa, rather than increased densities of specialist detritivores. However, communities in streams with reach-scale leaf additions often had the opposite response to small-scale treatments (shade, leaves in baskets) than communities in control streams. Our results indicate that the potential benefits of reintroducing allochthonous subsidies are likely to be dependent on the current composition of the target community, particularly the relative proportion of trophic specialists versus generalists.

Introduction

Stream food webs typically depend on energy from both local autochthonous (in-system) productivity and allochthonous inputs of terrestrial leaf litter (Baxter *et al.* 2005). Human activities, such as agricultural land-use intensification, alter the availability of allochthonous and autochthonous energy sources in streams (Hagen *et al.* 2010). Agricultural streams often suffer reduced allochthonous inputs due to removal of riparian vegetation (England & Rosemond 2004; Kominoski & Rosemond 2012), but increase in autochthonous production and become eutrophic in response to increased sunlight and nutrient run-off (Hagen *et al.* 2010; Burrell *et al.* in press). Eutrophication has been linked to changes in stream invertebrate community composition (Slavik *et al.* 2004), notably declines in species and trophic diversity, and shifts towards less sensitive/pollution-tolerant taxa (Harding *et al.* 1999; Verdonschot *et al.* 2012). Furthermore, eutrophic streams are often characterized by high abundances of defended herbivores; these unpalatable consumers create trophic bottlenecks which prevent energy from reaching predators at the top of the food web (Davis *et al.* 2010, Chapter Two).

Re-planting of riparian vegetation is often promoted as a tool for urban and agricultural stream restoration, with the expectation that increased shading will reduce autochthonous growth and enhance allochthonous inputs (Sweeney 1993; Quinn *et al.* 2007; Collier *et al.* 2009; Kominoski & Rosemond 2012), which will in turn support greater invertebrate diversity (Haapala *et al.* 2003; Moore *et al.* 2004). Although multiple studies have documented significant shifts in invertebrate community composition along gradients of forest cover (Quinn & Hickey 1990; Stone & Wallace 1998; Benstead *et al.* 2003; Death & Collier 2010), there have been relatively few empirical investigations of the effectiveness of riparian restoration in improving stream invertebrate communities (Parkyn *et al.* 2003; Greenwood *et al.* 2012), or the specific role of allochthonous resources in driving community changes (Lake *et al.* 2007).

Strong links between allochthonous resource availability and invertebrate community composition have been observed in experiments excluding leaf litter from forested streams where invertebrate abundance, diversity, and production subsequently declined (Wallace *et al.* 1999; Eggert & Wallace 2003). The strong response of invertebrate communities to allochthonous resource removal (Wallace *et al.* 1999; Eggert & Wallace 2003), suggests that resource limitation may be at least partly responsible for the loss of diversity commonly observed in eutrophic streams (Gafner & Robinson 2007; Evans-White *et al.* 2009, Chapter Two). However, it is still unclear whether reintroducing allochthonous resources will subsequently enhance invertebrate community diversity, especially in degraded agricultural streams which have lacked riparian vegetation and allochthonous subsides for many years. The few studies which have tested the effects of increasing allochthonous subsidies focused primarily on detritivore populations (Richardson 1991; Dobson & Hildrew 1992; Kominoski & Pringle 2009), rather than community-level effects, such as biodiversity (but see Szkokan-Emilson *et al.* (2011)).

The aim of this study was to investigate the effectiveness of reintroducing subsidies as a community restoration tool, particularly for lowland agricultural streams. Our objectives were three-fold. Firstly, we tested whether restoring allochthonous subsidies would improve community composition and enhance diversity. The second objective was to test whether altering the balance between

autochthonous and allochthonous resources was more effective in creating the desired shifts in community composition than addition of allochthonous resources alone. Here we were interested in whether the reintroduction of an allochthonous energy pathway was sufficient to reduce trophic bottlenecks associated with defended autochthonous consumers, or was it necessary to reduce autochthonous production and autochthonous consumer dominance for allochthonous reintroductions to have an effect? The third objective was to compare the impact of local, or small-scale, versus reach-scale resource additions on stream invertebrate communities.

We tested the effects of allochthonous resource additions on community structure by comparing the invertebrate communities which assembled in rock baskets of varying combinations of autochthonous and allochthonous resources. We hypothesised that restoring allochthonous resources would increase invertebrate abundance, diversity, and evenness, resulting in improved stream health and community metric scores. Specifically, we predicted that providing an alternative resource would aid less competitive consumers and detritivores, as well as their predators, thus breaking up the dominance by defended herbivores. We further hypothesised that limiting autochthonous production through shading while simultaneously adding allochthonous resources would result in the greatest increases in invertebrate diversity and evenness by further reducing defended consumer populations, as reported by Stone & Wallace (1998) in an investigation of stream community response to forest succession post-logging. Lastly, we predicted that large-scale leaf additions would have a greater effect than small-scale additions because the large leaf packs would attract additional invertebrates and reduce drift (Dobson & Hildrew 1992; Hinterleitner-Anderson *et al.* 1992) in treatment reaches.

Methods

The study was conducted in six streams in the Canterbury Plains region of the South Island of New Zealand. All six streams were within a 20 km area near the town of Rangiora (Figure 4.1). The Canterbury Plains are located between the eastern coastline and the Southern Alps on alluvial outwash plains of glacial origin (Webb 2008). The dominant land use is pastoral farming (Winterbourn 2008), and intensification of sheep and dairy farming has been increasingly rapid over the last twenty years (MacLeod & Moller 2006; Greenwood *et al.* 2012). Extensive networks of small streams cross the Canterbury Plains, but have become inextricably mixed with agricultural drains and irrigation or stock water races (Winterbourn 2008; Greenwood *et al.* 2012). Many of these streams, including our study sites, have been cleared of riparian vegetation, artificially straightened, and channelized. The six streams were chosen to be as similar as possible (Table 4.1), and divided into two sets: three streams in which allochthonous subsidies would be added (treatment) and three that would not receive experimental subsidies (control).

Experimental design

The relative abundances of autochthonous and allochthonous resources were manipulated in a short-term three-level split-split plot experiment (Figure 4.2). At the smallest scale of manipulation, we added detrital resources (leaves) at a patch scale (individual rock baskets), alongside control patches with no added resources. Half the baskets containing leaves and half the baskets with-

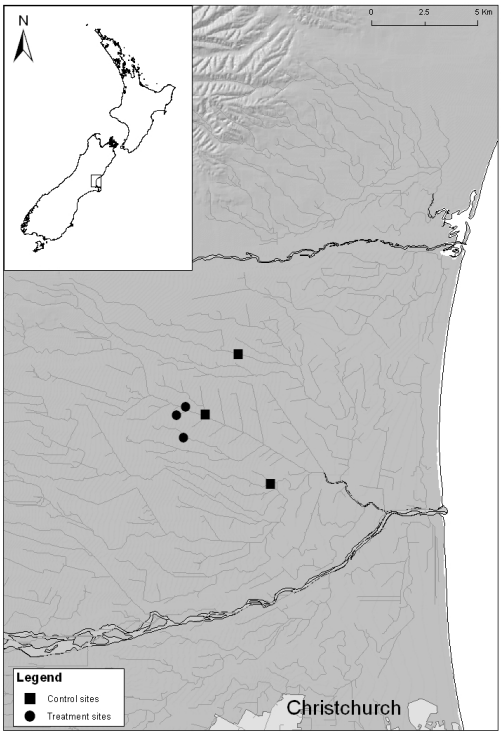

Figure 4.1: Location of six experimental streams within the Canterbury region, South Island, New Zealand. Treatment streams which received reach-scale leaf additions are indicated by circles, while unmanipulated control streams are represented by squares.

out leaves were artificially shaded to reduce algal growth, simulating the effect of riparian canopy shade on in-stream autochthonous production. Three of the six streams were randomly chosen to also receive reach-scale leaf additions, in which large (250 g) leaf packs composed of mixed native and exotic species (to reflect the most commonly occurring riparian vegetation in Canterbury; Meurk (2008)) were installed every 1.5 meters along a 200 metre reach (total of 133 leaf packs per reach, 33 kg of leaves per stream). Leaf packs were attached by twine to stakes driven into the

Table 4.1: Physical characteristics and productivity measurements for each stream with respect to reach-scale leaf litter additions. The letters in brackets after the stream name indicate whether the stream received reach-scale leaf additions (T, treatment) or was a control stream with no additions (C). Fine sediment cover refers to particles smaller than 1 mm, and GPP is gross primary productivity, or stream metabolism.

Stream	Width (m)	Depth (cm)	Velocity (m/sec)	Median particle size (cm)	Fine Sediment Cover (%)	GPP (mg O_2/m^2/day)	Chl-*a* (mg/m^2)
Ashworths (T)	2	41	0.14	1.5	29%	3.6	7.9
Ohoka (T)	1.7	14	0.12	2	7%	2.6	8.8
Plasketts (T)	2.2	26	0.28	3	9%	7.1	8.2
Hicklands (C)	1.7	25	0.24	3	9%	2.1	3.7
Jeffs Drain (C)	1.2	15	0.14	2	15%	0.2	7
Southbrook (C)	1.8	39	0.24	3	4%	0.3	2.6

stream bed and secured by large rocks. We also added 400 large rocks (approximately 20 – 40 cm in length) to each treatment stream reach, to help anchor leaf packs and retain organic matter within the treatment reach. Twenty-four hours after the large leaf packs were added, twelve small (24.5 x 15.5 x 6.5 cm) plastic baskets filled with an assortment of fist-size cobbles were placed in each of the six streams for macroinvertebrate colonization. The cobbles were pre-dried to eliminate any previous algal growth. In each stream, six rock baskets were placed underneath a 50 cm x 50 cm shadecloth hung just above the water surface in the center of the stream channel and six baskets were placed nearby in the center of an un-shaded section of stream channel. In each set of six baskets, three baskets contained 5 grams of leaves below the top layer of rocks (to prevent leaves from washing away). Thus, each stream had three replicates of all shade/leaves combinations: shaded with leaves, shaded without leaves, unshaded with leaves, and unshaded without leaves. The baskets were placed at the downstream end of the 200 metre reach, just within the treated area of large-scale treatment streams, to maximize exposure to upstream particulate organic matter released from the large leaf packs. To characterize pre-existing differences in community composition, three Surber samples were taken in each treatment and control stream prior to the start of the experiment. Small leaf packs (6 g) were also placed in each treatment stream to examine invertebrate colonisation of leaf packs. The baskets and small leaf packs were left in situ for six weeks; the short time scale was intended to allow for re-assemblage of the current invertebrate community according to resource availability while avoiding longer-term (*i.e.* seasonal) changes in community composition.

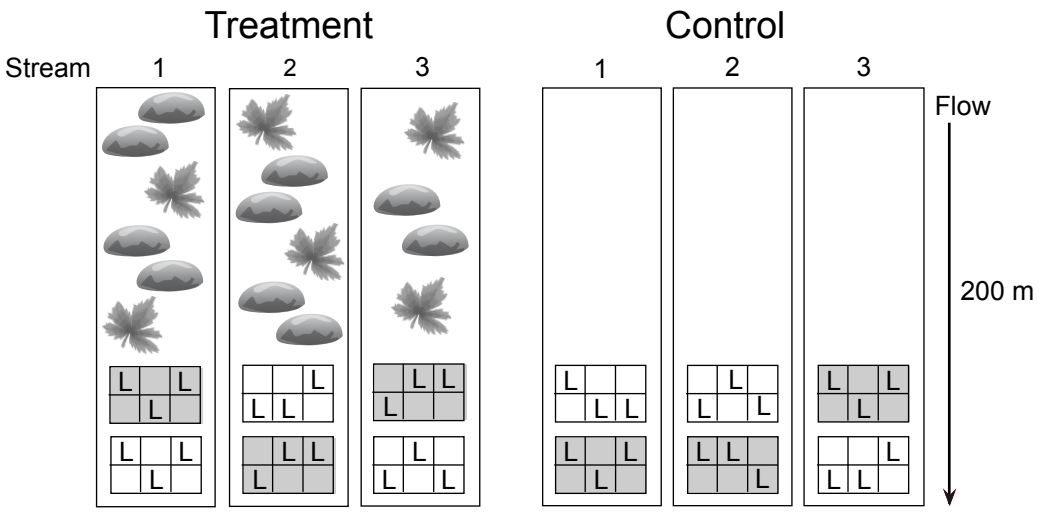

Figure 4.2: Split-split plot experimental design layout for the manipulations of leaves at two spatial scales and stream shade. Three treatment streams received reach-scale leaf additions, indicated by the leaves, and large rocks in the stream channel. Three control streams had no leaf or rock additions. Nested within each stream was a shaded section (gray box) and an un-shaded section (clear box), and nested within each shaded or un-shaded area were six rock baskets, three of which contained leaves (L). All baskets were placed just above the downstream limit of the reach.

Laboratory analysis

Upon removal from the streams, baskets were immediately placed in sealed plastic bags and transported to the laboratory, where the full contents of each basket was rinsed into a 500 μm sieve and sorted into invertebrates, remains of experimentally-added leaves, other particulate matter, and rocks. Macroinvertebrates were preserved in ethanol and identified using Winterbourn *et al.* (2006) and unpublished keys (B. Smith, NIWA, Hamilton, New Zealand). All macroinvertebrates in the collected leafpacks were similarly sorted and identified. The particulate matter collected in the 500 μm sieve from each basket (excluding the leaves initially added as an experimental treatment) was similarly dried, ashed, and re-weighed to determine the amounts of organic and inorganic particulate material which had accumulated in each basket over the course of the experiment.

Five cobbles from the top layer of each basket were retained to determine algal biomass using hot ethanol extraction chlorophyll-*a* analysis (Sartory & Grobbelaar 1984). Five cobbles were also collected from upstream of each treatment reach to test for pre-existing differences in algal biomass between treatment and control streams. Each cobble was immersed in a known volume of ethanol and placed in a water bath at 78˚C for 5 minutes, then removed and refrigerated in the dark for 12 – 18 hours. Chlorophyll-*a* concentration in the ethanol extract was measured using either a spectrophotometer (UV-1800, Shimadzu, Tokyo, Japan) or a flourometer (Trilogy Laboratory Fluorometer, Turner Designs, Sunnyvale, California, USA), depending on the concentration of the sample; the spectrophotometric method is most useful for chlorophyll-*a* concentrations greater than 100 μg/L, while the flourometeric method is most useful for samples below 200 μg/L. If visual assessment was insufficient to determine the correct method, samples were run using both techniques. Algal biomass was calculated as chlorophyll-*a* per square meter (Steinman *et al.* 2007) by multiplying the chlorophyll-*a* concentration by the surface area of the cobble, which was calculated using three axis measurements (Graham *et al.* 1988).

Statistical analysis

Analyses were conducted using a series of linear mixed effects models. Mixed effects models were chosen because they account for the nested structure of our experiment and because they are robust to unbalanced designs (Pinheiro & Bates 2000); our factorial design was disrupted by the loss of two baskets during the course of the experiment, and the loss of eight chlorophyll-*a* samples due to leakage during the laboratory extraction process. The mixed effects models were run in R (R Development Core Team 2013) using the lme function in the 'nlme' package (Pinheiro *et al.* 2013).

The first set of models tested for pre-existing differences in community composition between treatment and control streams. An array of response variables from the Surber samples collected in every stream prior to the start of the experiment were compared, including: rarefied richness, evenness, dominance, percentage and abundance of EPT (pollution-sensitive taxa: Ephemeroptera, mayflies; Plecoptera, stoneflies; and Trichoptera, caddisflies), and the New Zealand quantitative macroinvertebrate community index, QMCI (Boothroyd & Stark 2000). Variables were transformed as necessary to meet assumptions of normality prior to analysis, and invertebrate richness was rarefied to account for differences in abundance between treatments (Heck *et al.* 1975). Mod-

els were run with treatment as a fixed effect and stream as a random effect, as we were interested in differences between treatment and control stream groups, but not differences between individual streams. An identical model was also used to test for pre-existing differences in algal biomass.

The second set of models tested the impact of our experimental manipulations on the community metrics mentioned above. Algal biomass and organic and inorganic particulate matter were also tested to investigate differences in resource and habitat availability. Treatment (reach-scale leaf additions), shade, and leaves (within baskets) were included in the model as fixed effects, while leaves within shade within streams were included as random effects to indicate spatial nestedness (Pinheiro & Bates 2000; Crawley 2007). The nested experimental design was advantageous because it allowed testing for interactive effects between manipulations at different spatial scales. However, the drawback of such nested analyses is that power differs between levels, as does the variation associated with random factors (*i.e.* lower power and larger variation when testing at the level of streams as replicates, rather than baskets)(Quinn & Keough 2002). Backwards stepwise-regression with likelihood ratio tests using maximum likelihood estimation was used to sequentially remove non-significant terms until the most parsimonious model was reached (Zuur *et al.* 2009). A term was considered a significant effect if its removal reduced the predictive power of the model, at a cut-off value of $P = 0.05$. Occasionally this led to inclusion of terms which did not have significant p-values in the final model, which was re-fit by restricted maximum likelihood estimation (Zuur *et al.* 2009). However, because mixed-effects models have lower power at higher levels (Quinn & Keough 2002), we chose to retain all effects indicated as significant contributors to model fit by the stepwise regression procedure to minimize possibility of Type II errors.

We used the coefficients from this set of models to create plots of significant main effects and interaction terms (as indicated by the model simplification procedure) using the R package 'effects' (Fox 2003). The coefficients are a more realistic description of our results because the model incorporates the pseudo-replication inherent in the nested experimental design, which a calculation of means would not. However, the coefficients represent the fixed effects only, and the variation associated with the random effects is not included in the error bars (Fox 2003). Thus, while we have included the plots as a useful visual representation of the model results, they must be interpreted with caution, particularly when the error associated with the random effects, which is not represented on the plot, is likely to be large. Random effect variation was larger when models included only higher level terms, making streams the unit of replication (*i.e.* reach-scale treatment and shade manipulations).

The third set of models was used to test for differences in invertebrate community composition (richness, evenness, dominance, percent EPT, and QMCI) between the baskets and the reach-scale leaf packs in treatment streams. For these models, sample type (*i.e.* leaf pack or basket) was included as a fixed effect and sample type within stream as the random effect, because there were three replicates of each sample type within each stream. Only un-shaded baskets without leaves were included in the comparison, as this combination was effectively one of no manipulation and therefore most similar to natural stream conditions pre-experiment. The influence of the experimental treatments on community composition was assessed using multivariate analysis. Because each stream started with a unique community, we used partial redundancy analysis (pRDA) to test the influence of the experimental manipulations on community composition when the underly-

ing variation between streams was removed ('partialled out'). Abundance data was Hellinger-transformed prior to analysis to downweight the influence of rare species (Legendre & Gallagher 2001). Similarity percentages were used to determine which species contributed most to dissimilarities between treatments. The pRDA was done in R (R Development Core Team 2013) using package 'vegan' (Oksanen *et al.* 2012).

Results

There were no pre-existing differences in community metrics between treatment and control streams based on the Surber samples collected prior to the start of the experiment (all $P > 0.05$; Table B.1). Similarly, there was also no pre-existing difference in chlorophyll-*a* concentrations between treatment and control streams ($F_{1,4} = 1.23$, $P > 0.05$; Table B.1).

There were significant interactions between the reach-scale leaf additions and the basket-scale shade and leaf additions for several of the community metrics (richness, evenness, and dominance), whereas invertebrate abundance and percent pollution-sensitive EPT taxa were influenced by multiple manipulations individually but not by interactions between treatments (Table 4.2). There were no significant shade by leaves interactions, suggesting that the relative abundance of resources did not influence community composition, contrary to our prediction that simultaneously reducing autochthonous production and enhancing allochthonous production would have a larger effect than either manipulation alone. There were also no significant three-way interactions, therefore only the two-way interaction plots are presented (Figures 4.3, 4.4, 4.5).

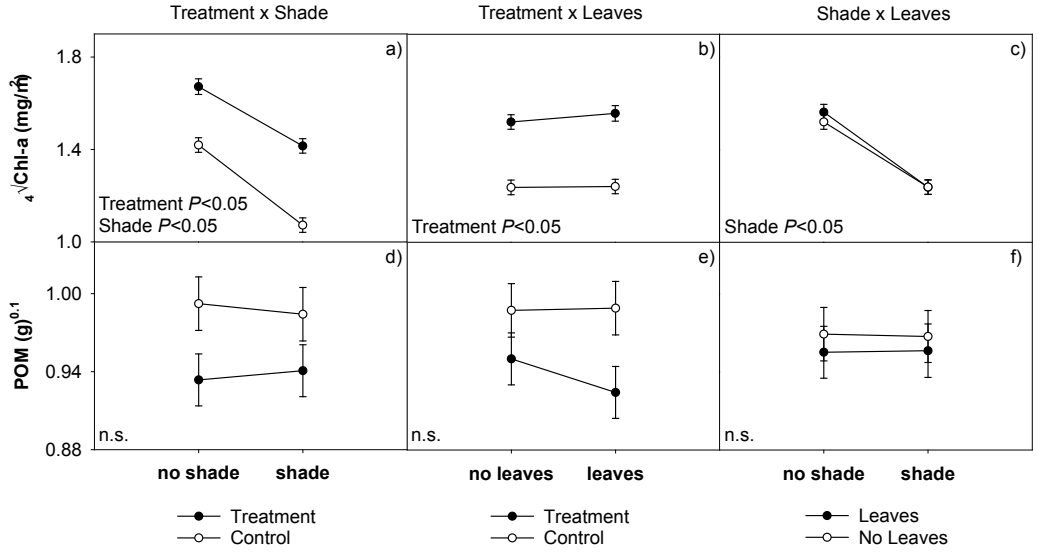

Figure 4.3: Two-way interaction plots illustrating the effect of reach-scale leaf-addition treatments (Treatment), shading (Shade), and basket leaf additions (Leaves) on (a-c) algal biomass, mg/m^2 chlorophyll-*a*, and (d-f) particulate organic matter, g POM, in experimental rock baskets. Points are the coefficients of fixed effect interaction terms (± 1 standard error) from the linear mixed effects models in Table 4.2. Error bars do not include random effects, and therefore are an under-estimate of the true variation.

Table 4.2: Main and interactive fixed effects in linear mixed effect analysis of experimental manipulations on basal resources (algal biomass and particulate organic matter); invertebrate community structure (abundance, richness, evenness, dominance); and stream health metrics (percent pollution-sensitive Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa, EPT abundance, and QMCI, a compositional metric). The full model is described initially, followed by the final reduced model produced via backwards stepwise regression for each response variable. The likelihood ratio and probability (P) for the likelihood ratio test are given for each term in the final reduced model. The degrees of freedom for all likelihood ratio tests was 1. The degrees of freedom, F-statistic, and probability (P) for fixed effects in each final model are also given, although these were not the criteria used to determine significance of effects. F-statistics and probability (P) are not given for main effects which were also present in an interaction.

Response variable	Fixed effects	Likelihood ratio	Likelihood P	df	F	P
Full model	Treatment			1, 4		
	Shade			1, 4		
	Leaves			1, 8		
	Treatment x Shade			1, 4		
	Treatment x Leaves			1, 8		
	Shade x Leaves			1, 8		
	Treatment x Shade x Leaves			1, 8		
Algal biomass (chlorophyll-*a*) (Figure4.3a-c)	Treatment	9.73	0.002	1, 4	15.5	0.02
	Shade	12.37	0.0004	1, 5	16.15	0.01
Particulate Organic Matter (Figure 4.3d-f)	–	1.62	0.2			
Invertebrate Abundance (Figure 4.4a-c)	Treatment	4.92	0.03	1, 4	5.07	0.08
	Shade	11.14	0.0008	1, 5	26.57	0.004
	Leaves	12.93	0.0003	1, 11	15.43	0.002
Richness (Figure 4.4d-f)	Treatment x Shade	6.15	0.01	1, 4	6.79	0.06
	Treatment x Leaves	6.06	0.01	1, 10	6.29	0.03
Evenness (Figure 4.4g-i)	Treatment x Shade	9.84	0.002	1, 4	16.94	0.01
	Treatment x Leaves	6.5	0.01	1, 10	6.43	0.03
B.P. Dominance (Figure 4.4j-l)	Treatment x Shade	9.13	0.003	1, 4	13.36	0.02
	Treatment x Leaves	4.6	0.03	1, 10	4.32	0.06
Percent EPT (Figure 4.5a-c)	Shade	9.13	0.003	1, 4	13.36	0.02
	Leaves	4.19	0.04	1, 11	4.17	0.06
EPT Abundance (Figure 4.5d-f)	Shade	9.92	0.002	1, 5	21.16	0.006
QMCI (Figure 4.5g-i)	–	1.97	0.16			

Overall, the experimental treatments were successful in manipulating the relative availability of basal resources, but the extent of influence depended on the scale of the manipulations. The reach-scale treatment had a significant effect on algal biomass; chlorophyll-*a* was higher in treatment streams than control streams (Figure 4.3; Table 4.2). As expected, chlorophyll-*a* was also lower in shaded baskets than non-shaded baskets in both treatment and control streams (Figure 4.3; Table 4.2), but did not differ between baskets with and without small-scale leaf additions (Figure 4.3; Table 4.2). There were no significant two-way interactions between treatment, shade, and/or leaves affecting chlorophyll-*a*, indicating that the reach-scale treatment did not affect the responses of primary producers to the small-scale treatments. The amount of particulate organic matter (POM) in the baskets was not higher in treatment streams (Figure 4.3; Table 4.2), contrary to our prediction that the large leaf packs would serve as an additional source of POM. Particulate organic matter was also not affected by either of the small-scale additions of shade or leaves or interactions between treatments (Figure 4.3; Table 4.2).

Invertebrate abundance was affected by both shading and small-scale leaf treatments as well as the reach-scale treatment (Figure 4.4; Table 4.2). Invertebrate abundance was higher in treatment streams, supporting our hypothesis that the reach-scale leaf additions would increase invertebrate abundance. There were also no significant interactions between treatments affecting invertebrate abundance(Table 4.2). The un-shaded baskets had greater abundances of invertebrates, as did the baskets with leaves, in both treatment and control streams (Figure 4.4; Table 4.2). Richness, evenness, and dominance were all influenced by interactions between the reach-scale treatment and shade or leaves (Figure 4.4; Table 4.2), indicating that reach-scale treatment influenced community responses to the small-scale manipulations. In treatment streams, richness and evenness declined, while dominance increased, in shaded baskets compared to un-shaded baskets (Figure 4.4; Table 4.2) and in baskets with leaves compared to baskets without leaves (Figure 4.4; Table 4.2). By comparison, in control streams the small-scale manipulations had opposite effects. Richness was higher in shaded baskets than in un-shaded baskets (Figure 4.4; Table 4.2) and higher in baskets with leaves than in baskets without leaves (Figure 4.4; Table 4.2). Evenness was also higher and dominance lower in shaded baskets in control streams (Figure 4.4; Table 4.2), indicating that invertebrate communities were more diverse when algal production was supressed. Neither evenness nor dominance varied between baskets with and without leaves in control streams (Figure 4.4; Table 4.2).

Stream health metrics were affected by the small-scale treatments but not the reach-scale leaf additions, contradicting our prediction that stream health metrics would mirror community metrics. The percent and abundance of pollution-sensitive EPT taxa were influenced by both shade and the small-scale leaf additions (shade, Figure 4.5; leaves, Figure 4.5; Table 4.2), but the directions of the responses was opposite of our predictions. We expected there would be more EPT in shaded baskets due to lower algal biomass and therefore fewer herbivores. However, the percent of EPT taxa was lower in shaded baskets in both treatment and control streams (Figure 4.5) and lower in baskets with leaves added in treatment streams (Figure 4.5). The abundance of EPT taxa, on the other hand, was only affected by shade (Figure 4.5), indicating that the decrease in percent EPT in baskets with leaves was due to increases in abundance of other taxa, rather than declines in EPT. Both percent EPT and QMCI appear to have a treatment effect (Figure 4.5), but treatment

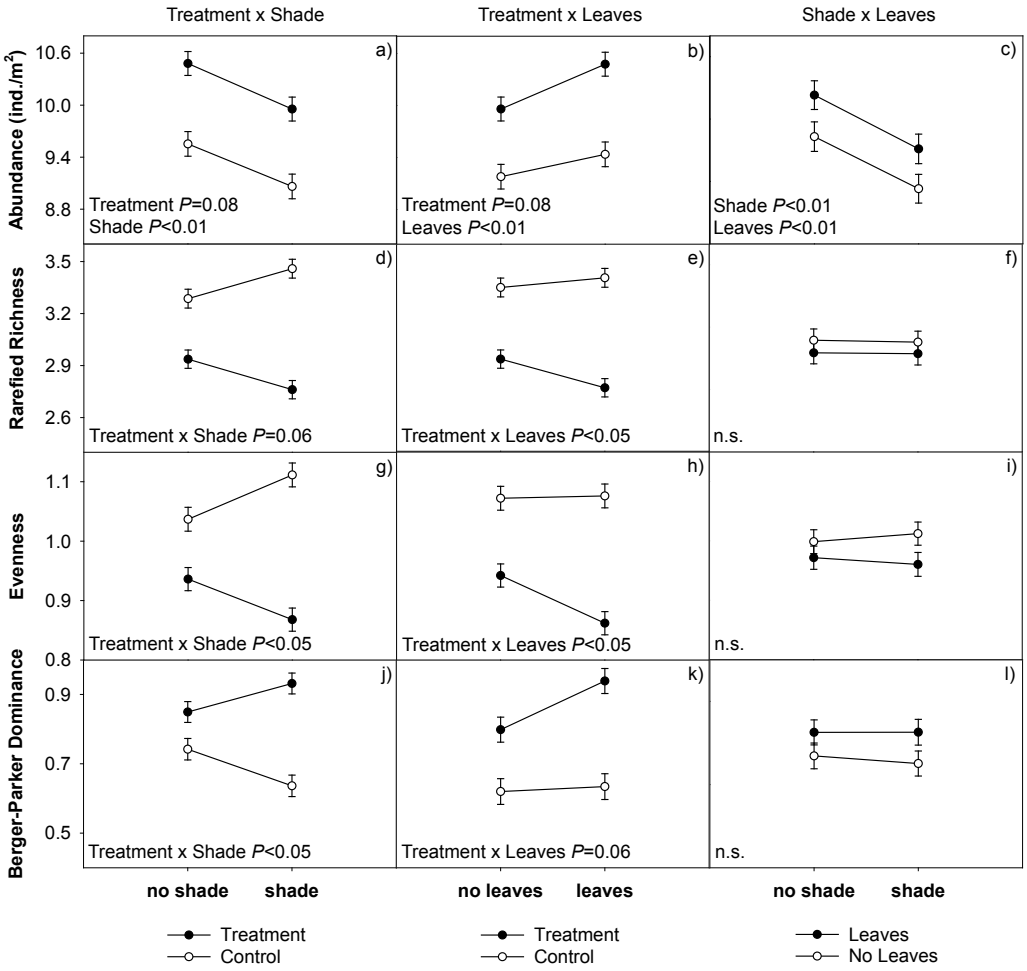

Figure 4.4: Two-way interaction plots illustrating the effect of reach-scale leaf-addition treatments (Treatment), shading (Shade), and basket leaf additions (Leaves) on (a-c) invertebrate abundance; (d-f) richness (rarefied, square-root transformed); (g-i) evenness (arcsine-square-root transformed), and (j-l) dominance (arcsine-square-root transformed) of invertebrate communities in experimental rock baskets. Points are the coefficients of fixed effect interaction terms ($\pm$ 1 standard error) from the linear mixed effects models in Table 4.2. Error bars do not include random effects, and therefore are an under-estimate of the true variation.

was not a significant contributor to model fit (Table 4.2), indicating that the random effects error component at the treatment level (which is not shown on the plots) was large for these variables (Table B.2).

Community composition did not vary greatly between reach-scale leaf packs and baskets (unshaded, without leaves) in treatment streams (Table B.3). The leaf packs had greater richness ($F_{1,2} = 61.65$, $P < 0.05$; Table B.3), but did not differ in evenness, dominance, percent EPT, or QMCI from the baskets (all $P > 0.05$; Table B.3), indicating that communities in leaf packs and communities in baskets had similar composition. Thus, it is unlikely that the lower diversity and higher dominance in baskets in treatment streams than in control stream baskets was due to preferential colonisation of reach-scale leaf packs rather than baskets in treatment streams.

Both shade and small-scale leaf additions were significant influences on community composition in the pRDA ($P < 0.01$; Figure 4.6), although differences between streams were responsible

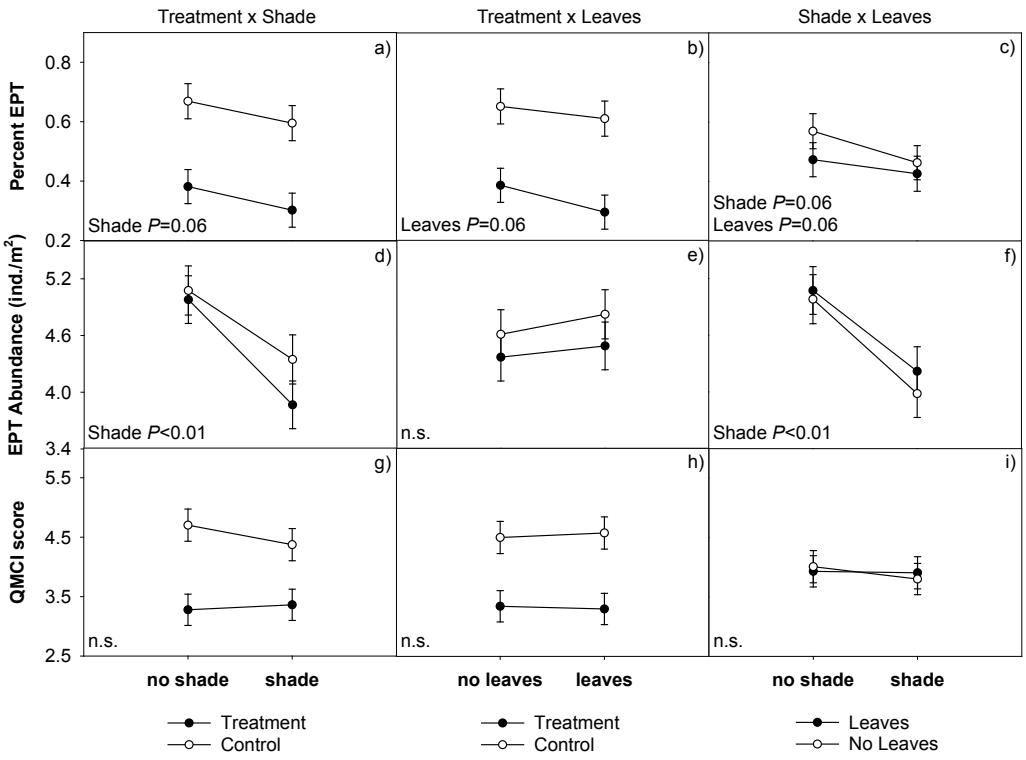

Figure 4.5: Two-way interaction plots illustrating the effect of reach-scale leaf-addition treatments (Treatment), shading (Shade), and basket leaf additions (Leaves) on (a-c) percent pollution-sensitive Ephemeroptera, Plecoptera, and Trichoptera (EPT) taxa (arcsine-square-root transformed); (d-f) EPT abundance (log-transformed); and (g-i) compositional metric (QMCI) scores of invertebrate communities in experimental rock baskets. Points are the coefficients of fixed effect interaction terms (± 1 standard error) from the linear mixed effects models in Table 4.2. Error bars do not include random effects, and therefore are an under-estimate of the true variation.

for the majority of the variation (68%). The first and second RDA axes explained 53% and 26% of the variation in community composition, respectively. Shade was strongly correlated with the first RDA axis (correlation=−0.87); basket communities in both treatment and control communities clearly separated into shaded and un-shaded along the first axis. Leaves, on the other hand, were associated with variation across multiple axes. Treatment was not strongly associated with either axis, and there was no distinct separation between treatment and control stream communities.

The changes in community composition between experimental treatments were driven primarily by a subset of fast-responding generalist taxa, particularly worms (Oligochaeta) and *Potamopyrgus* snails (Figure 4.7). The similarity percentage analysis confirmed that oligochaetes contributed the most to dissimilarities between community groups (treatments); oligochaetes on average contributed 12%, *Potamopyrgus* and *Deleatidium* contributed 8.9% and 8.6% respectively, followed by *Pycnocentrodes* (cased caddisflies) at 6.7% (Table 4.3). Oligochaetes were much more abundant in treatment streams (Figure 4.7) and had the largest contribution to differences between the reach-scale treatment and control communities (Table 4.3). *Deleatidium* and *Pycnocentrodes* were most influential in driving the shaded versus un-shaded dissimilarities in both Treatment and Control streams (Table 4.3); both taxa were more abundant in un-shaded treatments (Figure 4.7). *Potamopyrgus*, on the other hand, was associated most strongly with differences between small-scale

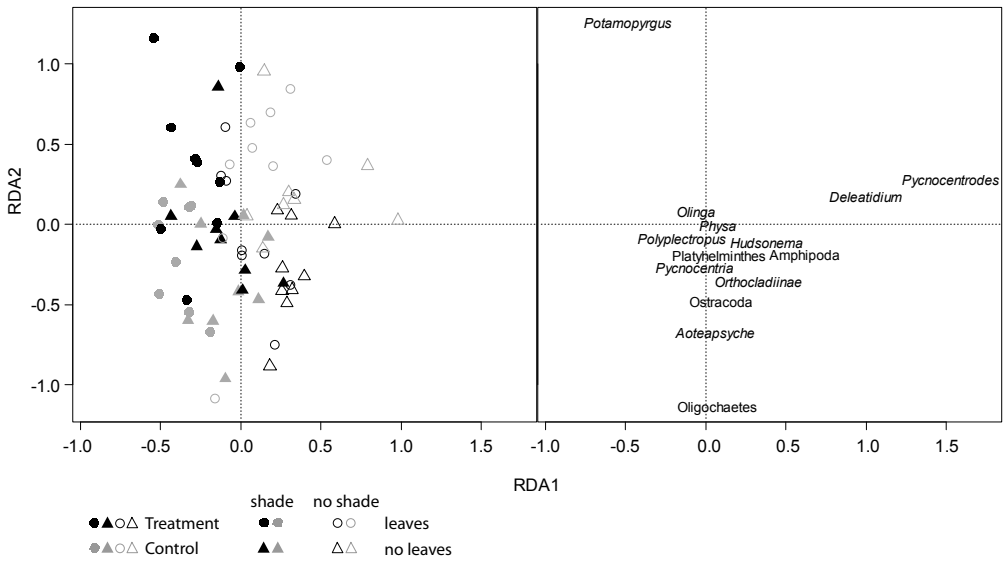

Figure 4.6: Partial redundancy (pRDA) ordination of community composition across all streams and experimental treatments. Points are individual rock baskets, black for samples from treatment streams with reach-scale leaf additions and gray for samples from control streams with no large leaf packs. Filled symbols indicate baskets which were shaded and open symbols un-shaded baskets. Circles indicate baskets which contained 5 grams of leaves mixed into the substrate and triangles those that did not have leaves. The corresponding distribution of common species with respect to the axes is shown on the second plot.

Table 4.3: Contribution of most common taxa to differences in community composition as estimated by similarity percentage analysis in each type of experimental treatment, as well as average contribution across all treatments.

Taxon	Treatment	Shade	Leaves	Average
Oligochaetes	12.4	11.9	11.9	12
Potamopyrgus	8.4	9	9.3	8.9
Deleatidium	8.4	8.8	8.7	8.6
Pycnocentrodes	6.5	7	6.6	6.7
Sphaeridae	5.3	5.4	5.4	5.4
Pycnocentria	5.9	4.8	4.8	5.2
Ostracoda	5	4.8	4.8	4.9
Hydropsyche	5.1	4.6	4.6	4.8
Physa	4	4.1	4.2	4.1
Amphipoda	3.6	4	3.9	3.8
Platyhelminthes	2.6	2.8	2.8	2.7
Psilochorema	2.6	2.3	2.3	2.4
Polyplectropus	2.2	2.5	2.4	2.4

leaf and no leaf treatments, and *Potamopyrgus* abundances were consistently higher in the baskets with leaves in both treatment and control streams (Figure 4.7). *Potamopyrgus* also made up the greatest fraction of the community in the leaf packs, although there was also a larger proportion of undefended taxa in the leaf packs than in the un-shaded baskets without leaves (Figure 4.7). Both *Deleatidium* and *Pycnocentrodes*, on the other hand, were relatively less abundant in the leaf packs than in the baskets (Figure 4.7). In general, the high abundances of snails in baskets with leaves and in leaf packs contradicts our hypothesis that providing allochthonous resources would

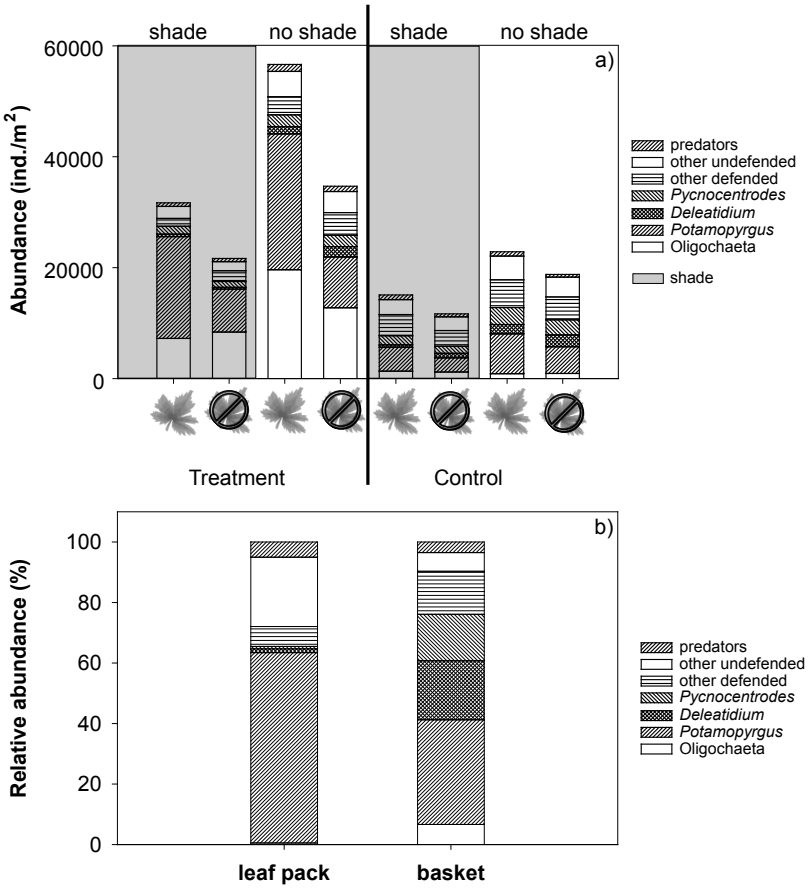

Figure 4.7: Abundance of most influential taxa (as indicated by similarity percentage analysis: Oligochaeta, *Potamopyrgus*, *Deleatidium* and Pycnocentrodes) and remaining organisms grouped into defended, undefended, and predators in (a) rock baskets within each experimental treatment and (b) in the reach-scale addition leaf packs and un-shaded baskets without leaves (to eliminate effects of small-scale manipulations) in treatment streams.

help reduce defended consumer/herbivore dominance.

Discussion

Allochthonous subsidies strongly influence recipient stream communities; removal of subsidies reduces macroinvertebrate abundance, diversity, and production (Wallace *et al.* 1999). Human land-use, particularly agricultural intensification, often involves the clearing of streamside vegetation, eliminating a key source of allochthonous material (England & Rosemond 2004; Kominoski & Rosemond 2012). While riparian planting is a common component of stream restoration efforts, the success of organic material reintroductions for improving community composition has rarely been tested (Parkyn *et al.* 2003; Greenwood *et al.* 2012). We assessed the effectiveness of allochthonous resource additions as a tool for restoring stream invertebrate communities in degraded agricultural streams. We found that relative resource availability influenced community assembly in eutrophic streams, but the effects varied depending on the spatial scale of the resource addition. Small-scale manipulations often had opposite effects on community metrics in streams with reach-scale leaf additions than in control streams. Differences in community composition

between treatments were largely driven by increased abundances of generalist taxa, primarily snails and worms. Overall, our results indicate that restoring resource diversity through allochthonous subsidies did not move community composition in the desired direction, and that the restoration of species diversity in eutrophic streams may be hindered by depleted species pools (Sundermann *et al.* 2011) and generalist and/or defended consumer dominance (Wootton 2002; Lake *et al.* 2007), which will require more than resource additions to improve.

Both shading and adding leaves at a small-scale had independent effects on invertebrate abundances and community metrics, but there were no interactions between shade and leaves, indicating that the relative balance between allochthonous and autochthonous resources did not influence community composition. Invertebrate abundances were lower in shaded baskets, which also had lower chlorophyll-*a*, and higher in baskets with leaves than in baskets without leaves. This suggests that invertebrate consumers were preferentially selecting patches of greater resource availability, regardless of the source (autochthonous or allochthonous). This also indicates that many taxa were generalist consumers, a common occurrence in deforested streams where invertebrates have already had to shift resource use from allochthonous to primarily autochthonous consumption (Benstead *et al.* 2003; Gothe *et al.* 2009). Contrastingly, studies conducted in forested regions report increases in specialist detritivore abundance with increasing allochthonous resource availability (Richardson 1991; Stone & Wallace 1998). Thus, our results suggest that generalist communities respond differently to shifts in resource availability than communities composed of a mix of generalists, herbivores, and detritivores. This is exactly why heavily impacted streams with a long history of degradation may not necessarily be improved as expected by traditional restoration strategies (Lake *et al.* 2007).

Surprisingly, the influences of shade and small-scale leaf additions on community metrics differed between streams that received reach-scale leaf additions and those that did not. In control streams without reach-scale leaf additions, the small-scale manipulations improved community composition as hypothesized. But when allochthonous resources were added at a large-scale, we observed declines in community metric scores in small-scale treatments. This begs the question: why did communities respond positively to the small-scale changes in resources but not to the reach-scale resource additions?

The reductions in diversity and increases in dominance associated with small-scale manipulations in treatment streams indicate that the reach-scale treatment may have created a "paradox of enrichment" situation. The paradox of enrichment refers to counterintuitive declines in biodiversity and population destabilization with increasing ecosystem productivity (Rosenzweig 1971). It has been suggested that the paradox is a consequence of differential responses between certain taxa or consumer groups to enrichment (Persson *et al.* 2001, Chapter Two). For example, defended taxa may increase disproportionately in response to enhanced resources because they are less vulnerable to predation (Leibold 1999; Persson *et al.* 2001). This mechanism was evident in our experiment as the different assemblage of invertebrate communities within small-scale treatments in treatment and control streams: baskets with leaf additions in control streams had greater invertebrate richness and community evenness than baskets without leaves, while in treatment streams communities in baskets with leaf additions had lower richness and evenness, but much higher dominance, than baskets without leaves.

The increases in dominance in treatment streams were largely driven by fast-responding generalist taxa, namely *Potamopyrgus* snails and Oligochaetes. *Potamopyrgus* were more abundant in baskets with leaves, and also in the leaf packs, where they made up over half the community. *Potamopyrgus* is known to be a strong competitor (Holomuzki *et al.* 2010) and to readily switch between a variety of autochthonous and allochthonous resources depending on resource availability (Parkyn *et al.* 2005). Thus, adding resources may simply have helped "the rich get richer," resulting in decreased diversity as exclusion of slower-responding, less competitive taxa was magnified, rather than reduced. This mechanism resolves the apparent paradox; diversity declined in treatment streams because the reach-scale leaf additions supported rapid expansion of *Potamopyrgus* populations, which then likely excluded other taxa. In control strams, however, the small-scale basket leaf additions were likley not enough to support large increases in dominant taxa, thus community composition improved with leaf additions.

Autochthonous production (algal biomass) was also elevated in treatment streams, which may have further contributed to the paradox of enrichment effect. The increase in algal biomass was potentially due to nutrient enrichment from dissolved organic matter leaching off the decomposing leaf packs, which has been shown to stimulate biofilm growth (Rounick & Winterbourn 1983; Olapade & Leff 2006), although it is unlikely that algae were nutrient-limited in these eutrophic streams. Alternatively, the increase in algal growth could be a consequence of reduced grazing pressure, as invertebrates in treatment streams are likely to have shifted their consumption to include more of the reintroduced allochthonous resources and associated microbial and/or fungal biofilms (Cummins 1974; Rounick & Winterbourn 1983; Tank & Winterbourn 1996; Simon *et al.* 2003). While we cannot distinguish whether increased leaf consumption or decreased competition for algae was responsible for the rapid increases in snail and worm abundances observed in this study, it was clear that their dominance was positively associated with resource availability and that these short-term responses drove changes in community composition among experimental treatments.

Our results suggest that invertebrate communities do respond to allochthonous resource additions, but that the effects of such additions may be limited by high proportions of defended generalist consumers, which are both resistant to predation (Wootton 2002; Davis *et al.* 2010, Chapter Two) and capable of shifting resources quickly (Winterbourn *et al.* 1984; Parkyn *et al.* 2005, Chapter Three). Furthermore, we found that allochthonous resource additions enhanced, rather than reduced, dominance. This has critical implications for restoration practice, as communities in agriculturally impacted/deforested streams are often already simplified and composed primarily of tolerant generalist taxa (Rahel 2002; Benstead *et al.* 2003; Lake *et al.* 2007, Chapter Three). Therefore it may be necessary to reduce dominance before reintroducing allochthonous resources in such systems. For example, we found that shade was associated with increased invertebrate community diversity and evenness as well as lower algal biomass in control streams, suggesting that reducing autochthonous production had a greater impact than resource additions on stream invertebrate communities. Including tree species with large canopies in riparian plantings is a potential long-term solution which would simultaneously add shade and provide allochthonous resources (England & Rosemond 2004). In the short-term, the dominant taxa could be targeted directly, either by removal of preferred habitat (*i.e.* macrophyte beds for *Potamopyrgus*; Collier

(2004)) or by introducing periodic hydrologic disturbances, as less mobile defended invertebrates are more susceptible to flood mortality than undefended taxa (Wootton *et al.* 1996; Lake 2000). Reducing dominance should not only improve community composition, but enhance community responsiveness to further rehabilitation efforts, and thus ought to be a key component of restoration for degraded, simplified communities with high proportions of generalist taxa, such as those found in eutrophic agricultural streams.

5

Population biomass accrual of key taxa enhanced by allochthonous resource additions

Abstract

Stream restoration projects have traditionally focused on increasing biodiversity via manipulations of in-stream habitat structure. However, this approach does not always result in the desired improvements in ecosystem health, suggesting that habitat is not the only factor preventing recovery, and that biodiversity may not be the most appropriate metric by which to monitor success. We proposed that targeting restoration on ecosystem functions and processes would result in greater improvements in ecosystem health than the standard habitat/diversity-focused approaches. To test these hypotheses, we conducted a stream restoration experiment designed to enhance population biomass accrual of benthic invertebrate communities through restoration of allochthonous subsidies, often a scarce resource in degraded lowland agricultural streams. Three streams were randomly chosen to receive the subsidy treatment while three additional streams were kept as control sites. The treatment consisted of 133 leaf packs, each containing 250 grams of dried leaves, attached to the stream bed in a 200 metre reach. We measured community metrics, such as composition and diversity, as well as population biomass accrual (secondary production estimated on a single date) and isotopic metrics of food-web structure, both before and one year after the leaf additions. The effect of the treatment was evaluated using before-after-control-impact (BACI) analysis to compare the differences in responses between control and treatment streams. Community metrics were highly variable and did not indicate improvements in community structure following allochthonous additions. However, population biomass accrual of key desirable taxa, such as pollution-sensitive bio-indicator species and predatory invertebrates, increased, indicating that the allochthonous additions improved resource partitioning and energy flow to higher trophic levels. These results suggest that targeting ecosystem processes is a useful strategy for stream restoration, and that function-based metrics may be more reliable indicators of restoration impact than changes in total biodiversity.

Introduction

As human impacts on the environment and global sustainability continue to grow (Tilman *et al.* 2011), the importance of rehabilitating impacted ecosystems is increasing (Roni *et al.* 2008). Freshwaters are some of the most threatened and degraded ecosystems on the planet, and biodiversity declines in freshwaters are more rapid than in any other ecosystem type (Sala *et al.* 2000; Dudgeon *et al.* 2006). In many countries stream and river restoration are now part of environmental policy (Lake *et al.* 2007), and billions of dollars are spent globally on restoration projects every year (Moore & Moore 2013). Traditionally, restoration has focused on the re-creation of habitat, with success measured as improvements in biodiversity (Palmer *et al.* 2010). However, this approach often falls short in two ways. Firstly, it assumes that restoring biodiversity will also result in improvements in ecosystem functions, the processes which contribute to the self-maintenance of ecosystems, such as biomass accrual, energy flow, and nutrient cycling (Thompson *et al.* 2012). Tight linkages between biodiversity and ecosystem processes have been observed in controlled experiments (Hooper *et al.* 2005), but it is still unclear whether a biodiversity-focused approach is the most effective strategy for restoration of natural ecosystems (Lake *et al.* 2007). Secondly, many impacted streams also have biotic constraints on recovery, such as intra- and inter-species interactions (Lake *et al.* 2007). These constraints are frequently associated with disruptions of ecosystem processes and functions, and are often not addressed by habitat restoration (Lake *et al.* 2007). For example, Kiffney (2008) reported that basal productivity and predation were stronger drivers of stream community diversity than physical habitat restorations. Restoring processes which underpin function is more likely to address the root causes of degradation and thereby incorporate multiple limiting factors (Beechie *et al.* 2010), thus overcoming many biotic constraints and enhancing restoration success. Moreover, ecosystems with restored functions should require less maintenance and be more resistant to future changes or disturbance (Beechie *et al.* 2010). Here we tested a restoration approach focused on improving function (energy flow) in lowland streams impacted by eutrophication and agricultural development.

Eutrophication, or extreme ecosystem productivity (Dodds 2007), is a common issue in agricultural waterways due to the removal of riparian vegetation, which increases photosynthesis through reduced shading (Hagen *et al.* 2010), and increased nutrient run-off, which further enhances in-stream plant growth (Dodds 2007). Agricultural streams are also often channelized, which reduces the retention of any allochthonous material that does enter the stream (Muotka & Laasonen 2002). As a result, eutrophic streams tend to have very high autochthonous (within-stream) production but few allochthonous (externally-produced) resources (Hagen *et al.* 2010). In association with this resource imbalance, fast-growing defended consumers frequently become dominant and form energetic bottlenecks of unpalatable biomass, disrupting energy flow to higher trophic levels and reducing predator populations (Davis *et al.* 2010, Chapter Two).

The goal of this study was to test whether restoring allochthonous resources would improve energy flow, thus alleviating some of the negative effects of eutrophication. Energy flow was measured as population biomass accrual of benthic invertebrates using a modified version of the traditional stream invertebrate secondary production method (Benke 1993; Benke 2010). Population to individual biomass ratios were also used as a measure of population turnover (Benke & Huryn

2010). Secondary production has frequently been used as a response variable in studies of pollution and/or environmental stress (Wallace *et al.* 1999; Shieh *et al.* 2002; Cross *et al.* 2005, 2006; Woodcock & Huryn 2007), but it has seldom been employed as a measure of ecosystem recovery (but see Entrekin *et al.* (2009)). This is surprising, given that secondary production is often described as "the most comprehensive measure of 'success' for a population (Benke 2010), due to its integration of multiple life history variables, including body size, density, growth, fecundity, and mortality. Thus, measuring population biomass accrual (*i.e.* modified secondary production), provides valuable insights into the recovery of individual populations as well as overall ecosystem function and energy flow.

We hypothesized that biomass accrual in eutrophic streams would be limited by bottlenecks of defended consumer biomass, and that these limitations could be reduced by adding allochthonous resources. Secondary production can be strongly driven by allochthonous resource availability; when leaf litter was experimentally removed from a forested headwater stream in North America for four years, total secondary production of the stream invertebrate community declined almost 80% (Wallace *et al.* 1999). The number of links within the food web also decreased after litter exclusion (Hall *et al.* 2000). We predicted that restoring allochthonous resources to eutrophic streams would create a trophic bottleneck bypass, or alternate energy pathway, and therefore enhance biomass accrual of previously excluded taxa, namely undefended primary consumers (*i.e. Deleatidium* mayflies) and predatory invertebrates. Correspondingly, we hypothesised that resource additions would create larger, more diverse, food webs due to a greater number of links between consumers and multiple basal resources (in contrast to Hall *et al.* (2000), where removal of a resource reduced the number of flows).

Methods

The experiment was conducted in six lowland streams on the Canterbury Plains, South Island, New Zealand. The Plains were formed from alluvial outwash of glacial origin (Webb 2008) and are located between the Southern Alps and the eastern coastline (see Chapter Four, Figure 4.1). The region has predominantly agricultural land-use (Winterbourn 2008) and has experienced rapid intensification of sheep and dairy farming in the past two decades (MacLeod & Moller 2006; Greenwood *et al.* 2012). The majority of small waterways within the Canterbury Plains, including our study sites, have been incorporated into or formed by extensive networks of agricultural drains and stock water races (Winterbourn 2008; Greenwood *et al.* 2012). The six study streams were chosen to be as similar as possible, both in terms of channel characteristics and agricultural impact, and all lacked riparian vegetation (Table 5.1).

Experimental design

Three randomly chosen streams received allochthonous subsidies, hereafter be referred to as "treatment" streams, while three reference, or "control," streams did not receive subsidies. In treatment streams, 250 gram leaf packs composed of mixed native and exotic leaves (to reflect the most commonly occurring riparian vegetation in Canterbury; Meurk (2008)), were installed every 1.5 metres within a 200 metre reach, for a total addition of 33 kg of leaves per reach. The leaf packs were

Table 5.1: Physical characteristics and productivity measurements for the three control and three treatment streams taken at the beginning (2011) and end (2012) of the allochthonous resource addition experiment. The letters in brackets after the stream name indicate whether the stream had leaf packs added (T, treatment) or was a control stream lacking allochthonous additions (C).

Stream	Width (m)	Depth (cm)	Velocity (m/sec)	Median particle size (cm)	Fine Sediment Cover (%)	GPP (mg O_2/m^2/day)	Chl-*a* (mg/m^2)
2011							
Ashworths (T)	2	41	0.14	1.5	29%	3.6	7.9
Ohoka (T)	1.7	14	0.12	2	7%	2.6	8.8
Plasketts (T)	2.2	26	0.28	3	9%	7.1	8.2
Hicklands (C)	1.7	25	0.24	3	9%	2.1	3.7
Jeffs Drain (C)	1.2	15	0.14	2	15%	0.2	7
Southbrook (C)	1.8	39	0.24	3	4%	0.3	2.6
2012							
Ashworths (T)	2	25	0.14	2	26%	10.8	34.8
Ohoka (T)	1.4	9	0.15	2	7%	7.8	35.7
Plasketts (T)	2.4	40	0.14	3	3%	13.8	20.3
Hicklands (C)	2.2	18	0.44	3	9%	3.4	13.5
Jeffs Drain (C)	1.7	30	0.06	2	9%	17.1	17.4
Southbrook (C)	1.6	49	0.23	3	4%	2.2	22.7

made of 6 mm mesh and anchored with twine to stakes driven into the stream bed, and replaced once during the experiment (for a total of 66 kg/200m/yr). Two large rocks (approximately 20—40 cm in length) were also placed every meter to serve as substrate for biofilm growth and to retain drifting organic matter. The experiment was designed as a before-after-control-impact (BACI) study, in which the changes in response variables in treatment sites (streams where subsidies were added) were contrasted to the changes in control sites (additional streams where no subsidies were added) over the same period (Underwood 1992). Although BACI analysis was developed as a technique to measure ecosystem response to perturbation, such as power plant discharge or similar point source pollution (Green 1979), it is equally well-suited to detecting impacts of restoration activities (Osenberg *et al.* 2006).

Field sampling and laboratory analyses

Each stream was sampled in April 2011, one week prior to the leaf additions, and in April 2012, one year after the leaf additions. Channel characteristics, including width, depth, median particle size and/or sediment type, presence or absence and type of macrophyte, and water velocity were measured at 10 points across 10 transects in each stream on both dates. Primary production was measured using the two-station diurnal oxygen curve technique for ecosystem metabolism and gross primary productivity (GPP) was calculated as production minus respiration and re-aeration (Bott 2007)(see Chapter Two for details). Algal biomass was determined using hot ethanol extraction chlorophyll-a analysis (Sartory & Grobbelaar 1984) on five cobbles collected randomly from within the stream reach (see Chapter Four for details).

Macroinvertebrate densities were measured using a Surber sampler (0.0625 m^2) with 250 μm mesh from three points, upstream, downstream, and the midpoint, along the 200 metre reach in each stream on both dates. Invertebrates were identified and counted in the laboratory under a

dissecting microscope (Nikon SMZ800, Melville, New York, USA), to the lowest practical taxonomic level (described in Chapter Two) using Winterbourn *et al.* (2006) and unpublished keys (B. Smith, NIWA, Hamilton, New Zealand). Several metrics of community structure were calculated using species abundances, including: rarefied richness (rarefaction corrects for differences in richness due to varying sample size (Heck *et al.* 1975), evenness, Berger-Parker dominance (Ravera 2001), percent pollution-sensitive EPT (Ephemeroptera, Plecoptera, and Trichoptera) taxa, and the New Zealand quantitative macroinvertebrate community index, QMCI (Boothroyd & Stark 2000). Taxa were also classified as either defended (*i.e.* with a hard case or shell) or undefended, and by functional feeding group: generalist collector-browsers, filter-feeders, scrapers, shredders, and predators (Winterbourn *et al.* 1984).

Calculation of biomass accrual

Biomass accrual of macroinvertebrates was estimated using the size-frequency method for secondary production (Benke *et al.* 1984; Benke 1996), but based on samples collected on a single date, rather than repeated temporal samplings (Benke 1996). This abbreviated method assumes that the size frequency distribution of a population on the sampling date was representative of the size frequency distribution for that population over the course of a year. Macroinvertebrates were photographed using a Leica stereomicroscope with digital camera and Leica Application Suite software (Leica M125/DFC 295, Leica Microsystems, Heerbrugg, Switzerland), and invertebrate body lengths (mm) were measured from the images using Adobe Acrobat X Pro (Adobe Systems Incorporated, San Jose, California, USA). The measurements from the three samples per stream were combined to create a single size frequency distribution for each taxon in a stream for each sampling date. If a sample contained more than 1000 individuals, it was split in half volumetrically and only half the sample was sorted and identified, and the number of length measurements doubled to accurately reflect the total sample abundance.

The size frequency distribution for each taxa was bootstrapped (sampled with replacement; Efron & Tibshirani (1993)) to produce 1000 data sets. Biomass accrual was calculated for each individual data set using published length-weight regressions (see Table C.1 for regressions and sources), resulting in 1000 estimates of biomass accrual, total biomass, and population to individual biomass ratios, or turnover rate. The biomass accrual estimates were corrected by the cohort production interval (CPI), or length of larval duration, for each taxa (Benke *et al.* 1984). CPIs can vary among individuals of a taxa as well as within a single taxa in different streams, and are often reported as a range between minimum and maximum values (Huryn 1996, 1998). To incorporate this inherent variability in the productivity estimate, a normal distribution of CPI estimates was constructed with 95% confidence boundaries set at the minimum and maximum reported CPI (primarily from Huryn (1996), but see Table C.2 for sources). The CPI distribution was randomly re-sampled to produce 1000 CPI values which were then used to correct the 1000 biomass accrual estimates. Finally, mean biomass accrual, total biomass, and turnover with 95% confidence intervals were calculated from the 1000 corrected biomass accrual values using the percentile method (Efron & Tibshirani 1993; Huryn 1996). Shredders were not present in sufficient numbers to construct a size frequency histogram and have been omitted from the analysis.

Stable Isotope Analyses

Macroinvertebrates were also collected with a kicknet (500 μm mesh) along the full length of the each stream reach on both sampling dates and frozen until preparation for stable isotope analysis. A subset of five taxa which were common and abundant across streams, and present at both sampling dates, were selected for isotope analysis. These taxa included representatives of the four main invertebrate functional feeding groups: generalist collector-browsers, filter-feeders, scrapers, and predators. Algae and leaf litter (both naturally occurring and from leaf packs in treatment streams on the 2012 sampling date) as well as submerged and emergent macrophytes, were collected as samples of possible basal resources. Sample preparation and analysis followed the same methodology given in Chapter Three.

Invertebrate stable isotope ratios were used to calculate food web metrics as well as determine consumer diets via a mixing model. An ANOVA followed by pairwise Tukey comparisons confirmed that the isotope signatures of the collected potential resources (algae, leaves, macrophytes) were distinct (ANOVA: $F_{3,44} = 54.66$, $P < 0.001$; Tukey: all $P < 0.05$) and could therefore all be included in the model. Both the mixing model and isotopic food web metrics were calculated using the 'SIAR' package (Parnell & Jackson 2011) in R (R Development Core Team 2013), as described in Chapter Three.

Statistical Analysis

Shifts in community composition over the course of the experiment were investigated using community dissimilarity indices. Pairwise dissimilarity indices were calculated for each site over time (before and after the experiment) using function vegdist with Euclidean distances on Hellinger-transformed species abundances in R package 'vegan' (Oksanen *et al.* 2012). Hellinger transformation reduces over-weighting of rare species and is recommended for use with Euclidean-based ordination methods (Legendre & Gallagher 2001). A Welch's *t*-test was used to compare changes in dissimilarity between treatment and control sites. To visualize the shifts in composition, the dissimilarity matrix was also plotted as a principal coordinates ordination using function wcmdscale in package 'vegan.' Because this ordination method is based on metric distance, the Euclidean distance between the two communities in ordination space is equivalent to the pairwise dissimilarity (Mardia *et al.* 1979).

The effect of the subsidy additions on community metrics, biomass accrual, and food web metrics (from stable isotopes) were assessed using a before-after-control-impact (BACI) analysis. We used an analysis of covariance (ANCOVA) with treatment and time as factors and ecosystem productivity as a covariate, because our previous work in similar eutrophic streams found strong relationships between productivity, community structure, and food web dynamics (Chapters Two and Three). Principal components analysis (PCA) was used to create a composite productivity variable including both gross primary productivity and algal biomass (see Chapter Two) for the covariate. Both gross primary productivity and algal biomass aligned with a single PCA axis, and together explained 80% of the variability among sites. Model simplification via backwards stepwise regression (Crawley 2007) was used to determine whether the covariate should be included in the model for a given response variable. A significant treatment by time interaction term in the

model indicated that the change in response variable was different between treatment and control streams, also known as a significant BACI effect. However, parametric statistics only indicate the probability of an effect, but not the magnitude, direction, or associated uncertainty (Osenberg *et al.* 2006) of the effect. As a result, low probabilities are often inaccurately interpreted as "no effect" (Osenberg *et al.* 2006). Thus, we did not adjust the statistical results to account for potential Type II statistical errors due to multiple comparisons. To further maximize our chances of detecting effects, we also calculated the effect size, or change in treatment versus change in control, for each response variable. Effect sizes are advantageous because they not only indicate the size and direction of an effect, but also give an indication of the variability (standard error), or uncertainty, about the response (Osenberg *et al.* 2006). Effect sizes were calculated as:

$$E = (T_A - T_B) - (C_A - C_B),$$

where T and C refer to treatment and control sites, respectively, and subscripts A and B refer to samples taken after and before the treatment (Stewart-Oaten & Bence 2001). The variability of the effect was calculated as ± 1 standard error. If there was a significant three-way interaction between productivity, treatment, and time in the BACI-ANCOVA analysis, effect sizes were adjusted for mean productivity using the centred covariate: (productivity – mean(productivity)). All analyses were done in R (R Development Core Team 2013).

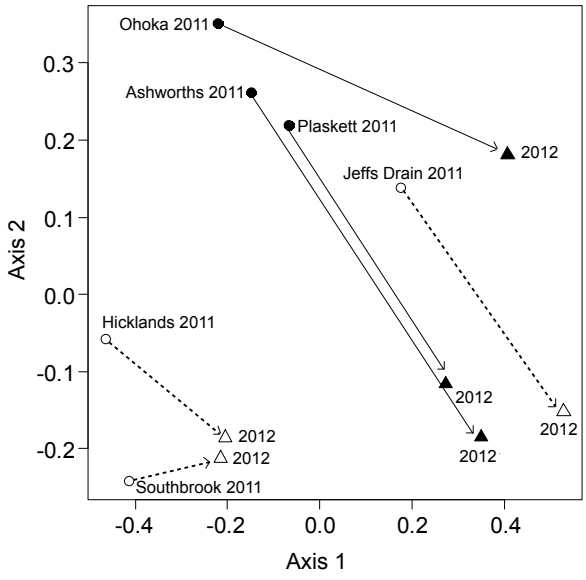

Figure 5.1: Principal coordinates ordination of invertebrate communities in treatment (black symbol) and control streams (white symbol) before (circles) and after (triangles) one year of allochthonous resource additions. The arrows between before and after communities indicate the distance and direction of community shift in ordination space over the course of the experiment; the length of the arrow is equivalent to the change in community dissimilarity.

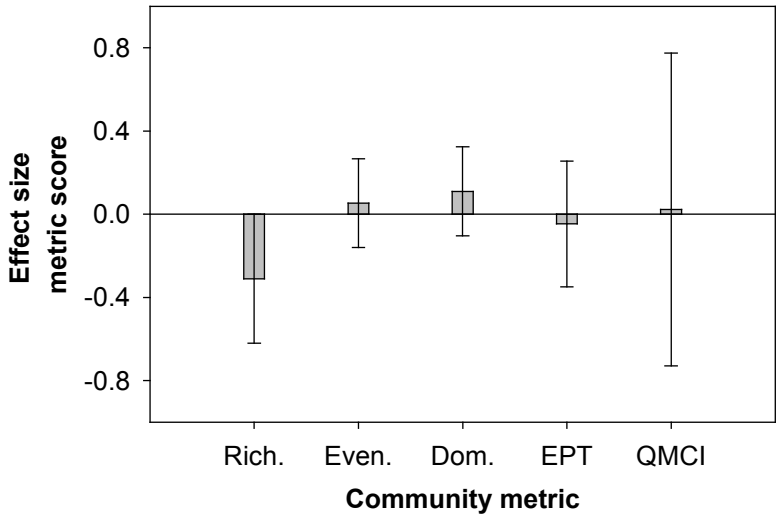

Figure 5.2: The mean (± 1 standard error) effect of experimental allochthonous resource additions on community diversity metrics: Rich., richness; Even., evenness; Dom., Berger-Parker dominance; EPT, the proportion of pollution-sensitive Ephemeroptera, Plecoptera, and Trichoptera taxa; and QMCI, the New Zealand Quantitative Macroinvertebrate Community Index score. Effect size was calculated as the difference between the changes in treatment (T) and control (C) streams before (B) and after (A) the experiment: $E = (T_A - T_B) - (C_A - C_B)$.

Results

Streams which received allochthonous subsidies had greater changes in community structure than control streams over the course of the experiment (Welch's t-test on dissimilarity: $t = 3.33$, $P < 0.05$), represented on a principal coordinates ordination as the generally larger distance between the 2011 and 2012 communities for treatment streams compared to control streams (Figure 5.1). Macroinvertebrate communities from both treatment and control streams moved along the first ordination axis, so this axis was most closely related to change over time. However, treatment sites also had larger shifts along the second ordination axis. Although this analysis does not indicate how composition changed (*i.e.*, improved or not), the greater change in dissimilarity in treatment streams indicates that our manipulation altered macroinvertebrate community composition.

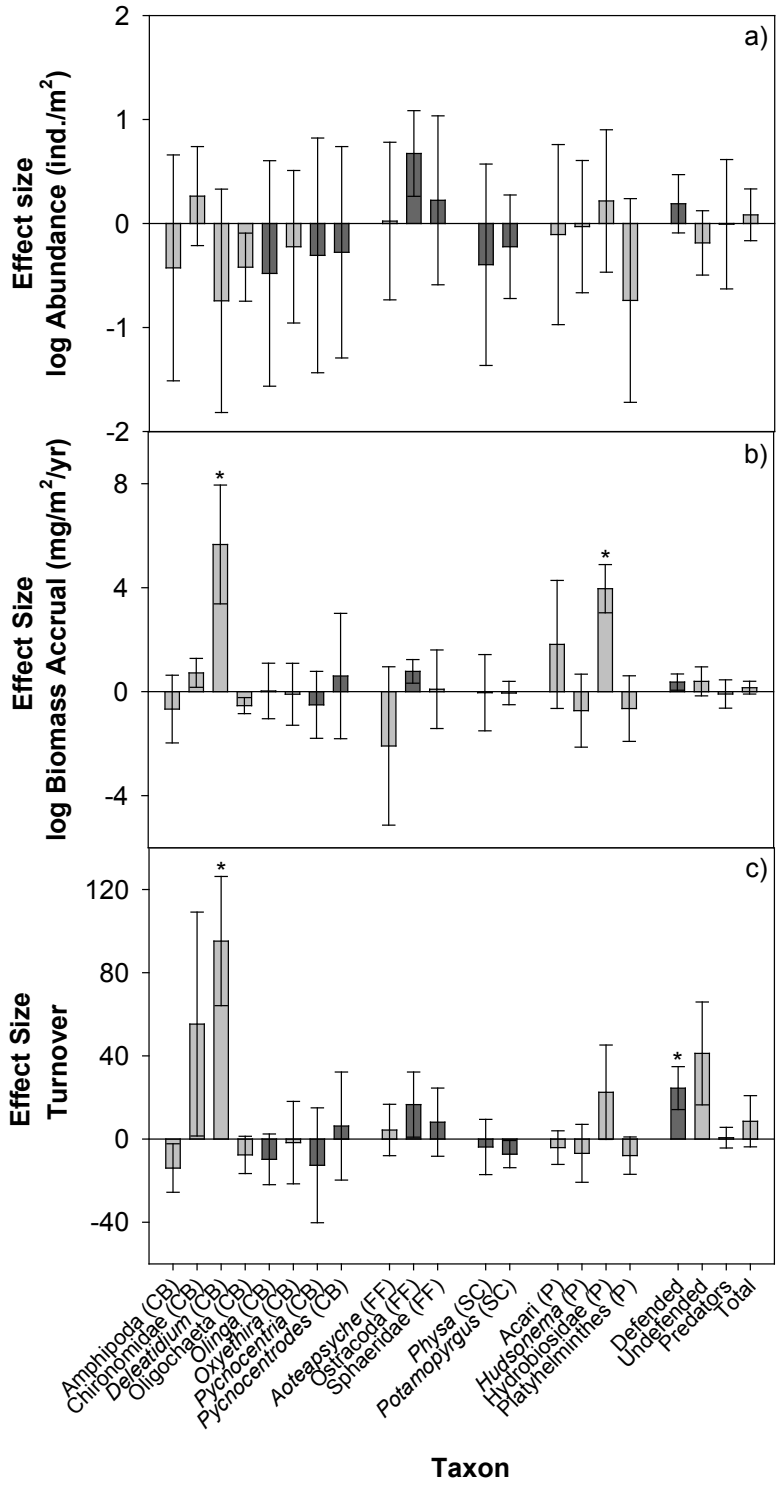

Figure 5.3: The mean (± 1 standard error) effect of experimental allochthonous resource additions on (a) abundance (ind./m^2), (b) biomass accrual (mg/m^2/yr) and (c) turnover of benthic macroinvertebrates. Effect size was calculated as the difference between the changes in treatment (T) and control (C) streams before (B) and after (A) the experiment: $E = (T_A - T_B) - (C_A - C_B)$. The darker bars indicate primary consumers with morphological defences against predations (*i.e.* a hard case or shell). The abbreviations in brackets after the taxa name indicate the functional feeding group of each taxa: P, predators; CB, collector-browsers; FF, filter-feeders; SC, scrapers/grazers. An asterix denotes the model for the response variable contained a significant treatment by time interaction term in the BACI-ANCOVA analysis.

There were few significant BACI effects, indicated by significant treatment by time interaction terms, in the BACI-ANCOVA analysis. However, the response variables which did have significant BACI effects were those with the largest effect sizes and the lowest variability (Table 5.2). Thus, the BACI model results, although more conservative, support an effect size-based approach and therefore we will focus on effect size responses to the allochthonous resource additions to maximize our chances of detecting possible effects. The community metrics were highly variable and did not differ greatly between treatment and control streams (Figure 5.2), contrary to our prediction that restoring allochthonous resources would improve diversity. The total abundance of invertebrates was also highly variable for all taxa (Figure 5.3). The only notable differences in abundance were an increase in ostracod abundance in treatment streams and a decline in oligochaete abundance (Figure 5.3), although the effect sizes were relatively small and neither taxa had significant BACI-ANCOVA treatment by time interactions (Table 5.2).

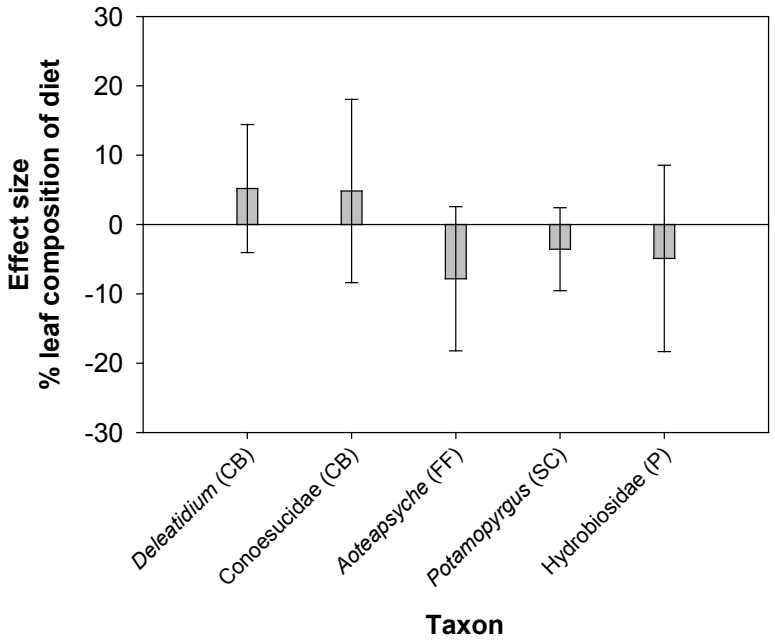

Figure 5.4: The mean (± 1 standard error) effect of allochthonous resource additions on leaf consumption by invertebrate taxa. Effect size was calculated as the difference between the changes in treatment (T) and control (C) streams before (B) and after (A) the experiment: $E = (T_A - T_B) - (C_A - C_B)$. The abbreviations in brackets after the taxa name indicate the functional feeding group of each taxa: P, predators; CB, collector-browsers; FF, filter-feeders; SC, scrapers/grazers.

Changes in biomass accrual were larger and less variable than the community metrics and abundance measurements. Contrary to our prediction, there were no changes in overall biomass accrual or turnover. However, key taxa, notably *Deleatidium* mayflies and hydrobiosid caddisflies, had greater biomass accrual and turnover in treatment streams (Figure 5.3), as well as significant BACI effects (treatment by time interaction): *Deleatidium* biomass accrual, $P < 0.05$; Hydrobiosidae biomass accrual, $P < 0.01$; *Deleatidium* turnover, $P < 0.01$. Ostracods and chironomids also increased in biomass accrual and turnover in treatment streams (Figure 5.3), but did not have significant BACI effects. Both defended and undefended primary consumers had increased

turnover in treatment streams, although only defended consumers had a significant BACI effect. Thus, while we did not see large changes in total biomass accrual or turnover, our hypothesis that allochthonous resource additions would enhance biomass accrual of previously excluded taxa was partially supported by a subset of taxa, including desirable species such as undefended primary consumers (*Deleatidium*) and predatory invertebrates (hydrobiosids).

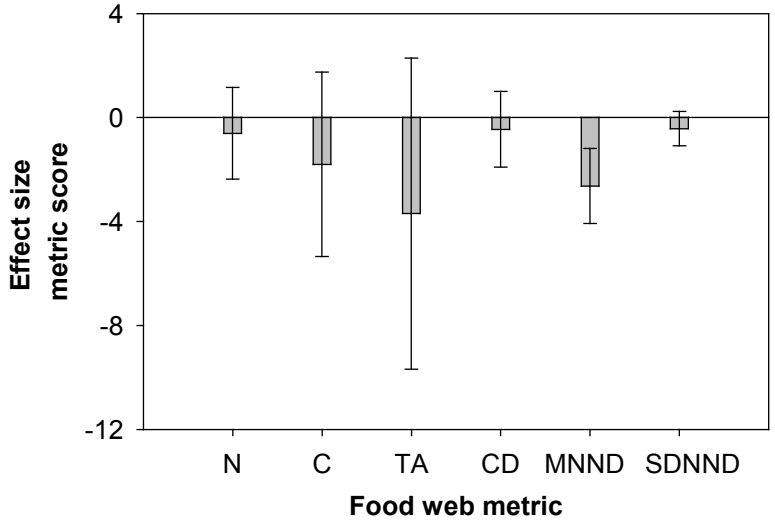

Figure 5.5: The mean (± 1 standard error) effect of allochthonous resource additions on isotopic food web metrics: N, nitrogen range; C, carbon range; TA, total area/trophic diversity; CD, mean centroid distance/average trophic diversity; MNND, mean nearest neighbour distance/density of species packing (trophic redundancy); and SNND, standard deviation nearest neighbour distance/evenness of species packing. Effect size was calculated as the difference between the changes in treatment (T) and control (C) streams before (B) and after (A) the experiment: $E = (T_A - T_B) - (C_A - C_B)$.

The stable isotope mixing model did not show any shift in invertebrate diets following allochthonous resource additions, due to large variability in isotope signatures (Figure 5.4). The isotopic food web metrics were also highly variable and only mean nearest neighbour distance (MNND), a measure of trophic redundancy, or niche packing, was substantially different between treatment and control streams, although it was not significant in the BACI-ANCOVA (Figure 5.5, Table 5.2). MNND declined in treatment streams, indicating increased redundancy, contrary to our prediction that food webs would become larger and more diverse following allochthonous resource restoration.

Discussion

Strong bottom-up effects of allochthonous subsidies on stream food webs have been demonstrated by declines in invertebrate abundance, production, and diversity following leaf litter exclusion (Wallace *et al.* 1997, 1999). The aim of our study was to test whether restoring allochthonous resources in agricultural streams, which have been lacking subsidies for many years, would in turn increase invertebrate population biomass accrual. Our results were typical of many stream restoration attempts because we saw no changes in diversity or other community metrics in re-

Table 5.2: Mean effect size, standard error (SE), and BACI-ANCOVA statistics for each response variable. The covariate indicates whether primary productivity was included as a multiplicative (x Prod) or additive (+ Prod) term in the BACI model. The *F*-statistic and probability (*P*) are given for the Treatment x Time term in the ANCOVA model. A significant Treatment x Time term (alpha of 0.05) indicates a difference in magnitude and/or direction of response between treatment and control samples. Degrees of freedom for each model were as follows: Treatment x Time x Prod: 1, 4; Treatment x Time + Prod: 1, 7; Treatment x Time: 1, 8.

Response variable	Covariate	Effect size	*SE*	*F* Treatment x Time	*P* Treatment x Time
Community metrics					
richness		-0.31	0.31	1	0.35
evenness		0.05	0.21	0.06	0.81
BP dominance	+ Prod	0.11	0.21	4.17	0.08
EPT		-0.05	0.3	0.02	0.88
QMCI		0.02	0.75	0.001	0.98
Invertebrate Abundance					
Acari (P)		-0.11	0.87	0.02	0.91
Amphipoda (CB)		-0.43	1.09	0.15	0.7
Hydropsyche (FF)		0.02	0.76	0.0009	0.98
Chironomidae (CB)	+ Prod	0.26	0.48	0.66	0.44
Deleatidium (CB)	+ Prod	-0.74	1.07	2.45	0.16
Hudsonema (P)	+ Prod	-0.03	0.64	0.68	0.44
Hydrobiosidae (P)	+ Prod	0.22	0.69	1.01	0.35
Oligochaeta (CB)		-0.42	0.33	1.64	0.24
Olinga (CB)		-0.48	1.08	0.2	0.67
Ostracoda (FF)		0.67	0.41	2.67	0.14
Oxyethira (CB)		-0.22	0.73	0.09	0.77
Physa (SC)		-0.4	0.97	0.17	0.69
Platyhelminthes (P)		-0.74	0.98	0.57	0.47
Potamopyrgus (SC)		-0.22	0.5	0.2	0.67
Pycnocentria (CB)	+ Prod	-0.31	1.13	1.13	0.32
Pycnocentrodes (CB)		-0.28	1.02	0.07	0.79
Sphaeridae (FF)		0.22	0.81	0.08	0.79
Defended		0.19	0.28	2.55	0.15
Undefended	+ Prod	-0.19	0.31	0.41	0.54
Predators	x Prod	-0.01	0.62	2.3	0.2
Total		0.08	0.25	0.1	0.76
Biomass Accrual					
Acari (P)	x Prod	1.82	2.46	0.02	0.9
Amphipoda (CB)		-0.67	1.3	0.26	0.62
Hydropsyche (FF)	x Prod	-2.09	3.05	0.002	0.97
Chironomidae (CB)	+ Prod	0.72	0.55	0.49	0.51
Deleatidium (CB)	x Prod	5.66	2.28	15.13	**0.02**
Hudsonema (P)	+ Prod	-0.73	1.4	1.87	0.21
Hydrobiosidae (P)	x Prod	3.96	0.93	39.74	**<0.01**
Oligochaeta (CB)		-0.54	0.31	3	0.12
Olinga (CB)		0.03	1.07	0.0006	0.98
Ostracoda (FF)		0.78	0.45	2.94	0.12

Response variable	Covariate	Effect size	*SE*	*F* Treatment x Time	*P* Treatment x Time
Oxyethira (CB)		-0.1	1.19	0.007	0.94
Physa (SC)		-0.04	1.47	0.0007	0.98
Platyhelminthes (P)		-0.65	1.26	0.27	0.62
Potamopyrgus (SC)		-0.05	0.45	0.01	0.91
Pycnocentria (CB)	+ Prod	-0.51	1.29	1.56	0.25
Pycnocentrodes (CB)	x Prod	0.6	2.41	3.81	0.12
Sphaeridae (FF)		0.09	1.51	0.004	0.95
Defended		0.37	0.31	1.41	0.27
Undefended	+ Prod	0.4	0.56	0.02	0.88
Predators	+ Prod	-0.09	0.54	1.37	0.28
Total		0.15	0.25	0.39	0.55
Turnover					
Acari (P)		-4.09	8.07	0.26	0.63
Amphipoda (CB)		-13.92	11.66	1.42	0.27
Hydropsyche (FF)		4.37	12.36	0.13	0.73
Chironomidae (CB)		55.31	53.83	1.06	0.33
Deleatidium (CB)	x Prod	95.21	31.04	33.6	**<0.01**
Hudsonema (P)	+ Prod	-6.86	13.92	1.59	0.25
Hydrobiosidae (P)	x Prod	22.5	22.7	4.34	0.1
Oligochaeta (CB)		-7.63	8.96	0.72	0.42
Olinga (CB)	+ Prod	-9.72	12.19	3.02	0.13
Ostracoda (FF)		16.59	15.65	1.12	0.32
Oxyethira (CB)		-1.72	19.81	0.008	0.93
Physa (SC)		-3.81	13.26	0.08	0.78
Platyhelminthes (P)		-7.95	8.97	0.78	0.4
Potamopyrgus (SC)		-7.22	6.54	1.22	0.3
Pycnocentria (CB)		-12.59	27.61	0.21	0.66
Pycnocentrodes (CB)		6.27	25.98	0.06	0.82
Sphaeridae (FF)		8.13	16.4	0.25	0.63
Defended		24.51	10.32	5.64	**0.04**
Undefended		41.19	24.72	2.78	0.13
Predators		0.67	4.95	0.02	0.9
Total		8.56	12.3	0.49	0.51
Invertebrate leaf consumption					
Deleatidium (CB)		5.19	9.24	0.32	0.59
Conoesucidae (CB)		4.84	13.22	0.13	0.73
Hydropsyche (FF)		-7.82	10.4	0.57	0.51
Potamopyrgus (SC)		-3.56	5.99	0.35	0.57
Hydrobiosidae (P)		-4.89	13.44	0.13	0.73
Food web metrics					
N-range		-0.6	1.77	0.12	0.74
C-range		-1.8	3.54	0.26	0.63
Total Area		-3.69	5.99	0.38	0.55
Centroid distance	x Prod	-0.45	1.46	4.98	0.09
MNND	x Prod	-2.63	1.44	5.41	0.08
SDNND		-0.43	0.66	0.42	0.54

sponse to our manipulations (Palmer *et al.* 2010). However, biomass accrual of key taxa, including undefended primary consumers, sensitive bio-indicator species (*Deleatidium*; O'Halloran *et al.* (2008)), and predatory invertebrates, increased following subsidy restoration, suggesting that allochthonous addition s did bypass trophic bottlenecks and/or reduce dominance of defended consumers, as we predicted. Thus, our results confirm that process-based restoration has potential to increase restoration effectiveness (Beechie *et al.* 2010), as well as the usefulness of ecosystem functions, such as biomass accrual (or secondary production) as tools for monitoring and assessing restoration (Brooks *et al.* 2002; Cardinale *et al.* 2002; Young & Collier 2009). Including biomass accrual as a response variable allowed us to detect several effects that would have been overlooked by community metrics-based analysis.

As is often the case in ecosystem-scale experiments, the high variability among streams and over time made it difficult to detect, let alone assess, effects of our allochthonous resource restoration (Osenberg *et al.* 1994; Entrekin *et al.* 2007; Hoellein *et al.* 2007). Functional measures (*i.e.*, biomass accrual) had both larger effects and less variability than either counts of invertebrate abundance or community metrics, and were therefore more useful as response variables for monitoring restoration impact. Similar comparisons between community and functional metrics, including primary production, respiration, and decomposition, to physical habitat (substrate heterogeneity) restoration also report that ecosystem function variables were more sensitive than community metrics (Brooks *et al.* 2002; Cardinale *et al.* 2002). Moreover, Young & Collier (2009) suggested functional measures would be more useful in identifying nonlinear responses to ecosystem impairment or restoration, and for early detection of small initial changes following restoration. Secondary production and biomass accrual, in particular, are advantageous response variables because they summarise several of the most important influences on community ecosystem function, including invertebrate life histories, community and ecosystem dynamics, resource partitioning, and total energy flow through a community (Benke 1993, 1996).

The taxa which had increased biomass accrual in treatment streams, *Deleatidium*, chironomids, and ostracods, were primarily small-bodied, fast-growing species (excepting hydrobiosids, which will be addressed later in the discussion). Small organisms tend to have short life cycles, fast growth, and produce multiple generations per year (Cross *et al.* 2005, 2006). As a result, they are able to rapidly exploit new resources and are often the first species to show population-level responses to changes in resource availability (Cross *et al.* 2005). This suggests that biomass accrual of longer-lived taxa would potentially also increase if the leaf additions were continued for multiple years.

The increases in biomass accrual of previously excluded taxa, such as *Deleatidium* and chironomids, are particularly promising because they suggest a shift in energy pathway in treatment streams. Decomposing leaf packs are a significant source of allochthonous fine particulate organic matter (FPOM) in streams (Hoffmann 2005), and *Deleatidium*, chironomids, and ostracods are all known to consume primarily FPOM of both algal and detrital origin (Winterbourn 2000; Cross *et al.* 2005; Chapman *et al.* 2011). Although stable isotope signatures were too variable to confirm whether invertebrates shifted diets following allochthonous additions, most New Zealand stream invertebrates are opportunistic generalists (Winterbourn 2000), and *Deleatidium* in particular has been shown to alter its consumption of alternate resources in accordance with resource availability

(Rounick *et al.* 1982; Parkyn *et al.* 2005). Cross & Benke (2002) showed that competitive interactions between consumers can result in lower growth rates and production of one or both populations. Consequently, the increased biomass accrual of these key taxa, and the absence of increases in biomass accrual by snails and oligochaetes, which were previously dominant in these streams (Chapter Four), suggests that the additions of alternative resources may have reduced competitive effects between primary consumers.

Deleatidium and chironomids are also important taxa within stream food webs because they are common prey for predatory invertebrates, particularly hydrobiosid caddisflies (Winterbourn 2000, Chapter Two). Predator production is strongly linked to the productivity of their prey (Wallace *et al.* 1997); thus, the concurrent increases in chironomid, *Deleatidium*, and hydrobiosid biomass accrual suggest that energy associated with the reintroduced allochthonous resources was being passed up the food web to higher trophic levels, as we predicted.

Despite these promising indications of improved energy flow in treatment streams, we did not see large changes in food web structure, contrary to our prediction that the addition of an allochthonous energy pathway would increase the number of links within the food web. Instead, we found that invertebrate primary consumer diets became more similar, indicated by increased trophic redundancy (lower isotopic mean nearest neighbour distance, MNND). Although counterintuitive, this result is not unlikely in communities dominated by generalist consumers, which is often the case in degraded streams (Benstead *et al.* 2003; Lake *et al.* 2007, Chapter Three). In a typical isotope study, the range of isotope signatures reflects niche diversification at the base of the food web, and various consumers will have distinct signatures reflecting their particular preferred resource (Layman *et al.* 2007). In a generalist community, however, when a new resource is added most organisms will begin to consume a mixed diet, causing isotope signatures to converge in the middle of the resource spectrum. As a result, while more allochthonous energy was going to desirable species, the vast majority of production was still made up by other taxa, and so the introduction of an additional energy pathway had little influence on food web structure.

Overall, the results of this study concur with recent claims that restoration projects can be improved by an increased focus on restoring and monitoring ecosystem functions (Beechie *et al.* 2010) and that stream restoration needs to expand from the traditional habitat-only approach to include other limiting factors, such as allochthonous resource availability (Lake *et al.* 2007). Furthermore, while we did not see any changes in total biodiversity, we have shown that focusing on specific ecosystem processes shows promise for achieving desired community outcomes, including reduced dominance of defended consumers and increased biomass of common prey species, such as chironomids and *Deleatidium* (McIntosh 2000), and predatory invertebrates, which are important restoration targets because they play a key role in regulating stream food webs through top-down processes (Holomuzki *et al.* 2010). Moreover, predatory invertebrates are often more susceptible to stress than smaller prey organisms due to their longer lifespans, larger size, greater bioenergetic demands, and are therefore also a good indicator of overall stream health and recovery (Quinn & Hickey 1990). Thus, functional metrics appear to be more sensitive and useful response variables for detecting effects of restoration (Cardinale *et al.* 2002; Brooks *et al.* 2002; Young & Collier 2009). Additionally, targeting ecosystem functions is more likely to effectively address root causes of degradation (Lake *et al.* 2007; Beechie *et al.* 2010) by incorporating multiple

biotic and abiotic constraints (Ehrenfeld & Toth 1997), such as a lack of allochthonous resources and corresponding trophic bottlenecks and competitive interactions.

6

Discussion

Food webs integrate community ecology, the study of patterns in species richness, abundance, and composition, with ecosystem ecology, which focuses on the flow of materials and energy within and between ecosystems, and thus are a powerful framework for investigating the mechanisms which regulate ecosystem structure and function (Thompson *et al.* 2012). My results indicate that studying food webs will advance understanding of the complex problems which face ecologists today, such as maintaining healthy, functioning ecosystems under increasing anthropogenic stress, including eutrophication of freshwaters (Allgeier *et al.* 2011; Woodward *et al.* 2012). In this chapter I will discuss the insights gained by investigating the effects of eutrophication on ecosystem productivity, diversity, and function from a food web perspective. Firstly, I will summarise my results on the effects of eutrophication and changes in resource availability on stream communities. Secondly, I will examine the implications of my findings for general ecological theory, including food web stability and ecosystem functioning, and highlight new questions which have arisen during the course of my research. Thirdly, I will discuss how the insights gained from studying food-web responses to eutrophication can be applied to guide and improve stream restoration and management.

Effects of eutrophication on stream communities and food webs

Eutrophication is often defined simply as an increase in trophic state or primary productivity (Dodds 2007). However, I found that "productivity" actually includes multiple variables; both gross primary productivity (GPP) and algal standing stock were independent sources of productivity in streams (Chapter Two). From a food web perspective, eutrophication may be more accurately described as an increase in autochthonous resource availability. Moreover, the causes of eutrophication, such as land-clearing for agriculture, often result in a simultaneous reduction of allochthonous resources (Hagen *et al.* 2010), another important source of energy for many stream food webs (Cummins 1975).

These shifts in resource diversity influence stream communities through two key food web mechanisms: changes in composition (Vannote *et al.* 1980; Rosi-Marshall & Wallace 2002, Chap-

ter Two) and altered trophic interactions, including changes in consumption of basal resources (Rounick *et al.* 1982; Benstead & Pringle 2004; Parkyn *et al.* 2005, Chapter Three) as well as interactions between organisms, such as predation, apparent competition and/or exclusion (Leibold 1999; Davis *et al.* 2010, Chapter Two). Changes in composition and trophic interactions in turn influence the flow of energy throughout the food web (Wootton *et al.* 1996; Taylor *et al.* 2006; Davis *et al.* 2010). I found that the effects of increasing productivity on community composition, namely diversity and relative abundance of functional groups, varied between sources of productivity and among trophic levels (Chapter Two). Defended consumers showed the largest response; they increased in relative abundance more than any other taxa or functional group (Chapter Two). Leibold (1999) similarly reported that nutrient enrichment produced algal communities dominated by grazer-resistant forms, while undefended, fast-growing algae were more abundant in low nutrient ponds. I also found that changes in composition influenced the trophic interactions between organisms, and thus energy flow through the food web (Chapter Two). All functional groups increased their consumption of autochthonous carbon as productivity increased, but rates of switching varied, indicating that some organisms were faster or more effective at adapting to the change in resources (Chapter Three). Those that shifted early may have then competitively excluded less generalist taxa. Alternatively, the increase in defended consumers, which are less preferred by predators, may have increased predation on undefended prey, further exacerbating their decline in high productivity streams (Leibold 1996, Chapter Two).

Despite shifts in primary consumer composition and diet, the increased production did not flow up the food chain to higher trophic levels (Chapters Two and Three), indicated by the lack of increase in trophic height, a common measure of food chain length, in response to increasing autochthonous energy availability (Chapter Three). This was at least partially due to altered trophic interactions associated with shifts in composition, namely the increased abundance of defended consumers, which may have served as a trophic bottleneck by trapping energy in unpalatable biomass (Chapter Two). Increases in predator-resistant prey in nutrient-enriched streams (Davis *et al.* 2010) and in rivers undergoing flow regulation (Wootton *et al.* 1996) resulted in similar disruptions in energy flow up the food web, suggesting that defended consumer bottlenecks are not uncommon in freshwater ecosystems.

Although there was no increase in trophic height, food webs expanded horizontally with increasing productivity, as taxa spread out in niche space (Layman *et al.* 2007, Chapter Three). This suggested that the communities in highly productive streams were composed primarily of generalist consumers capable of re-focusing on different components of autochthonous production (Chapter Three), such as algal particles of different size or position in the biofilm matrix (Tall *et al.* 2006a). As a result, changes in diet maintained (and increased) food web breadth, but not trophic height, across the productivity gradient.

Given that the shifts in food web structure and community composition in eutrophic streams were strongly associated with resource homogenization (Chapters Two and Three), I tested whether experimentally reintroduced allochthonous resources, in the form of leaf litter, improved energy flow and community structure (Chapters Four and Five). However, I found that changes in composition following leaf litter additions were also largely driven by increased dominance of generalist taxa (Chapter Four), in contrast to the increases in allochthonous specialist densities follow-

ing leaf additions to forested streams in North America (Richardson 1991) and England (Dobson & Hildrew 1992). Interestingly, the effects of experimental allochthonous resource additions on food web structure (determined using the same isotopic metrics as in Chapter Three) were nearly the opposite of the changes that occurred with increasing autochthony. In Chapter Three, increasing autochthonous production was associated with increased food-web breadth and greater trophic diversity, while in Chapter Five food webs in treatment streams receiving increased allochthonous resources had greater trophic redundancy than nearby control streams where resources were not manipulated. Although the results of both studies were somewhat counterintuitive, given the predictions of food web theory, namely that greater resource diversity should support more diverse, reticulate food webs (Moore *et al.* 2004; Kominoski *et al.* 2010), each is consistent with what might be expected from generalist-dominated communities. For example, a community containing specialists at each end of the autochthonous-allochthonous resource spectrum would contract towards one end of the spectrum as resources were lost and expand when resources were restored (Stone & Wallace 1998). In a generalist community, on the other hand, organisms are likely to respond to resource homogenization by re-focusing within the single remaining resource, increasing niche partitioning (Tall *et al.* 2006a), but when both autochthonous and allochthonous resources are available, most organisms will consume a mixture of the two resources (Rounick *et al.* 1982; Winterbourn 2000), causing niches to expand and isotope signatures to re-converge. Thus, I found that food webs consisting primarily of generalist consumers do not respond to changes in resource availability in the same way as diverse food webs containing a range of resource specialists.

Experimental allochthonous resource additions in eutrophic streams affected food web structure not only through shifts in the position of nodes within food web, but also via changes in the number and strengths of links. For example, secondary production of desirable taxa, including sensitive indicator taxa and their predators increased in streams with allochthonous additions, whereas they did not increase in response to increasing autochthonous production across a eutrophication gradient (Chapter Two). This suggests that competition among primary consumers had been reduced and trophic bottlenecks bypassed by the experimental addition of an alternate energy pathway (Chapter Five). Therefore, my results indicate that while restoring resource diversity may not improve community diversity in generalist-dominated degraded streams, it can improve ecosystem function and energy flow to higher trophic levels, thereby alleviating some of the negative impacts of eutrophication on stream food webs (illustrated in Figure 6.1).

Implications for ecological theory

As indicated by the unexpected changes in food web structure, very few of my results conformed to straightforward extrapolations of theory. I suspect this was largely due to two factors: oversimplified theories and degraded, generalist-dominated, invertebrate communities. Firstly, my food-web approach highlighted the importance of including influences on both species and trophic interactions, whereas both productivity-diversity theory (Waide *et al.* 1999; Mittelbach *et al.* 2001) and biodiversity-ecosystem function theory (Hooper *et al.* 2005; Thompson *et al.* 2012) were originally developed based on a single trophic level. In contrast, I found different productivity-diversity

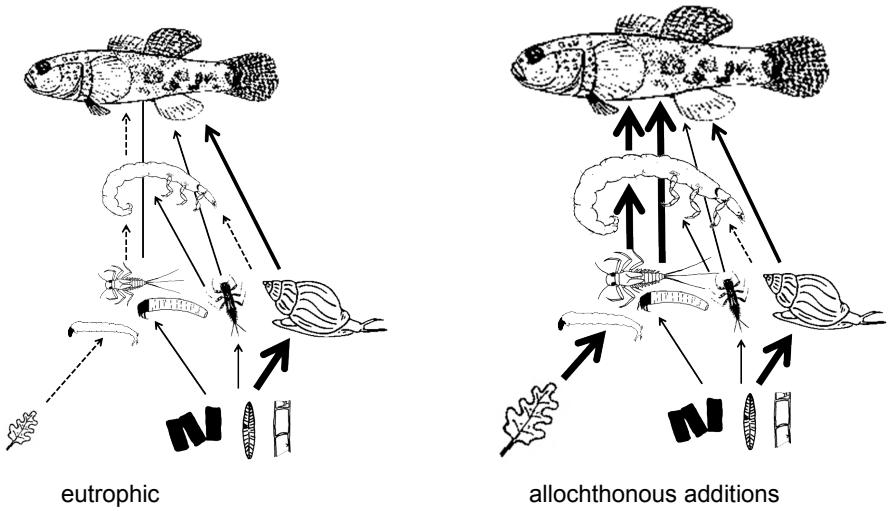

Figure 6.1: Illustration of a trophic bottleneck in a eutrophic stream food web and improved energy flow after allocthonous resource additions. The width of the arrows indicates the relative strength of the pathway, whereas dashed lines represent a lost pathway. Organisms represent various functional feeding groups; the size of the organism represents the relative abundance/biomass of that group.

relationships between trophic levels, due to multiple consumer and responses to multiple sources of productivity (Chapter Two), rather than the single linear or unimodal response which is generally predicted (Mittelbach *et al.* 2001). Furthermore, although I found only linear productivity-diversity relationships, my results indicate that productivity-diversity relationships are mediated by species composition and trophic interactions, and thus could potentially take a variety of shapes, depending on which species and interactions dominate in a given ecosystem.

I also did not find that greater productivity supported longer food chains (Chapters Two and Three), as predicted by simple energetic theory (Pimm 1982; Schoener 1989; Post 2002b). The lack of increase in food chain length is likely due to the formation of trophic bottlenecks composed of unpalatable defended consumers in high productivity streams (Chapter Two). For example, Wootton *et al.* (1996) similarly reported that a reduction in floods led to an increase in sessile defended grazers, which in turn reduced energy available to predators, and predator occurrence and abundance declined. Post & Takimoto (2007) have also proposed that changes in omnivory control the effect of productivity on food chain length. If that is the case, changes in omnivory, could simply be negating the positive influence of productivity on food chain length. This omnivory mechanism likely occurs in conjunction with trophic bottlenecks; as energy becomes trapped in unpalatable primary consumer biomass, predatory invertebrates become scarcer, causing fish to feed lower in the food web. Therefore, the influence of eutrophication on food chain length is liable to vary with the extent of trophic omnivory and the occurrence of unpalatable defended consumers, both of which may prevent longer food chain lengths despite increased productivity.

Secondly, many theories assume that communities contain a mix of specialist and generalist taxa, the relative proportions of which will shift in response to resource availability and environmental change (Vannote *et al.* 1980). For example, community composition is predicted to shift with natural changes in resource availability longitudinally along a river network, from detritiv-

orous dominance in forested headwater reaches to greater relative abundances of herbivores and filter-feeders in large, open downstream reaches with more autochthonous production (Vannote *et al.* 1980; Rosi-Marshall & Wallace 2002). My research, on the other hand, was conducted in impacted streams (or for Chapters Two and Three, along a gradient of increasing impact), in which the species pools were already reduced to primarily tolerant, highly-adaptable, generalist taxa. Because communities were composed of generalists, changes in resource availability did not always have the predicted, or desired, effects. I was surprised to find, in Chapter Three, that food webs expanded with resource homogenization, and surprised again, in Chapter Five, when trophic redundancy increased after resource diversity was restored. However, as discussed previously, both results make sense for generalist-dominated communities.

Implications for food web stability

The discrepancy between my observations of generalist food-web responses to environmental changes and the responses predicted based on theoretical food webs rich in resource specialists raises several important theoretical and practical considerations. First and foremost, the unique responses I observed in generalist communities reinforces the need for better knowledge of the relative influences of species diversity, functional diversity, and trophic diversity on food-web stability and ecosystem function. Although I did not test food-web stability directly, current diversity-stability theories (McCann 2000; Huxel *et al.* 2002; Rooney & McCann 2012) predict that shifts in resource diversity as well as biodiversity will influence food-web stability.

Current consensus suggests diversity enhances stability (Rooney & McCann 2012), because if species are lost there is a greater chance there will be another species present able to still fulfil its role (McCann 2000; Naeem 2002). Others have also proposed that communities of generalists should be more stable, because food webs can rapidly restructure in response to environmental change (Valdovinos *et al.* 2010), buffering systems against losses of a particular resource or pathway (Woodward 2009). Interestingly, I found that increases in trophic diversity among generalists (Chapter Three), maintained food web structure in eutrophic streams. It remains to be determined whether such generalist food webs represent an alternative stable state, or if they remain less stable than more species diverse webs in un-degraded streams.

Food-web stability has also been linked to the diversity of basal resources (Huxel *et al.* 2002) and/or number of energy pathways (MacArthur 1955). However, this reasoning may not apply when food webs are based on a single, sub-divided resource, as in Chapter Three, rather than multiple resources. Recent food web models suggests that multiple resources are necessary for this logic to hold; multi-channel food webs have been shown to enhance stability most when the pathways are asynchronous, *i.e.* they differ in the amount of energy input and the rate at which it passes up the food web (Rooney *et al.* 2006). Slower processing of energy results in weaker interactions, thus greater resource diversity results in more weak interactions, which stabilises food webs against oscillatory responses to strong interactions in the fast channel (Rooney & McCann 2012). Allochthonous/detrital pathways have slower turnover than autochthonous pathways because detritus breaks down into many forms of varying lability during the decomposition process (Moore *et al.* 2004). Furthermore, allochthonous resources are donor-controlled, or density independent;

the rate of consumption has no influence on the rate of supply (Moore *et al.* 2004). Therefore, according to this theory, restoring allochthonous resources should have improved the stability of food webs in the treatment streams in Chapter Five. Indeed, I found that small increases in secondary production of predators in the treatment streams, indicating that energy flow to higher trophic levels had been restored by the alternative allochthonous pathway (Chapter Five), potentially bypassing the trophic bottlenecks observed in solely autochthonously-based food webs (Chapter Two). Thus, my results confirm that food webs with multiple energy pathways resulting from diverse resources are liable to be more stable than food webs based primarily on a single resource.

Interestingly, it has also been suggested that the degree of generalisation within a food web can influence the effect of changes in resource availability on food web stability. Huxel *et al.* (2002) found that model food webs composed largely of specialists were more stable at low levels of allochthonous subsidies due to reduced pressure on individual resources, whereas food webs comprised of generalists were more stable at high levels of resource addition. This is consistent with my finding of generalist dominance at high resource availability, for both autochthonous (Chapters Two and Three) and allochthonous (Chapter Four) resources. Thus, trophic specialization is likely to influence how resource additions affect food-web stability.

In general, my results are consistent with diversity-stability theory, and support recent advances which suggest that the diversity of trophic pathways is as important as organismal diversity (Huxel *et al.* 2002; Rooney *et al.* 2006), and that it is the structure of the links between species which ultimately confers stability (McCann 2000; Rooney & McCann 2012). Therefore, restoration approaches which aim to improve the diversity of energy pathways will result in more stable, sustainable communities capable of resisting further perturbations (Ehrenfeld & Toth 1997; Rooney & McCann 2012).

Implications for ecosystem function

Diversity has also been predicted to improve ecosystem function, the natural processes which maintain ecosystems, such as formation of biomass, carbon storage, nutrient cycling, decomposition, and transport of sediment or other materials (Woodward 2009; Thompson *et al.* 2012). Multiple experiments have demonstrated that ecosystem function and stability are enhanced by high biodiversity and reduced by declines in species diversity (McCann 2000; Hooper *et al.* 2005). The basic rationale for the effect of diversity on function is similar to the argument for the influence of diversity on stability: greater diversity is associated with greater redundancy, and therefore if a species is lost from a diverse community there are better odds that there will be another species present which will be able to maintain the function previously supported by the lost species (Hooper *et al.* 2005). My observations of ecosystem functions in relation to changes in diversity and community composition enable the evaluation of several of the proposed mechanisms.

'Diversity' actually refers to multiple characteristics of an ecosystem, and which definition of diversity is most relevant for biodiversity-ecosystem function relationships is debated (Hooper *et al.* 2005). The most specific interpretation of diversity is species richness, the number of different species in a community (Hooper *et al.* 2005), although recent research indicates that functional

traits, rather than species identity per se, drive biodiversity effects (Reiss *et al.* 2009). This hypothesis was supported by my results; I found that changes in the relative proportion of certain functional traits, namely morphological defences against predation, affected energy flow, as increased production only benefitted primary consumers, especially defended taxa, but did not reach higher trophic levels (Chapter Two). By this standard, the lack of increase in trophic height in Chapter Three indicates that function (energy flow) was not affected by the increases in trophic diversity, suggesting that in this case trophic diversity was not equivalent to functional diversity. On the other hand, generalists and their predators were also the first taxa to increase secondary production, another key ecosystem function, after allochthonous resources were reintroduced into eutrophic food webs (Chapter Five), indicating that the rapid adaptability of generalists can be beneficial for some functions. This observation raises an important caveat: different organisms will contribute more or less to a variety of ecosystem functions, which often creates a trade-off between functions and diversity, as some functions will be positively associated with certain species and negatively with others (Zavaleta *et al.* 2010). Some functions may be driven primarily by a few dominant species (Doherty *et al.* 2011), while others have been found to be correlated with species richness alone (Huryn *et al.* 2002). However, higher species richness has been found to reduce the trade-offs between functions and provides greater multifunctionality (Zavaleta *et al.* 2010).

Diversity can also be used more broadly to include species composition, such as relative abundance or evenness, and several studies have indicated that community composition is as equally important as species richness as a predictor of ecosystem function (Hooper *et al.* 2005). In fact, occasionally a single numerically dominant species can provide the majority of a certain ecosystem function (Smith & Knapp 2003; Doherty *et al.* 2011). Rare species, such as top predators or a key detritivore, can also have a disproportionate effect, in which case their loss will dramatically reduce ecosystem function (Taylor *et al.* 2006; Woodward 2009). In either situation, greater diversity improves the chances that key taxa will be present (Hooper *et al.* 2005). It has also been hypothesized that diversity may enhance ecosystem function via positive interactions among species, i.e. complimentarity or niche partitioning and facilitation (Hooper *et al.* 2005). However, as previously discussed, I found that increased trophic diversity did not appear to influence energy flow (Chapter Three).

Biodiversity-ecosystem function theory has largely focused on the effects of organismal diversity. I also tested the influence of resource diversity on ecosystem function, specifically secondary production of macroinvertebrates (Chapter Five). In this case it was predicted that restoring allochthonous resources would promote species diversity (Wallace *et al.* 1999; Moore *et al.* 2004), which would in turn improve ecosystem function (Hooper *et al.* 2005; Thompson *et al.* 2012). However, species richness did not change in streams which received allochthonous additions. Nonetheless, secondary production increased for a small subset of taxa. These results not only support the importance of community composition, rather than species richness alone, in driving ecosystem function, but indicate that resource diversity may play a role as well. It is highly probable that function, like stability, is enhanced by greater numbers of links, or energy pathways, and therefore also influenced by food-web interactions (Thompson *et al.* 2012).

Overall, a food web approach can advance our understanding of biodiversity-ecosystem function relationships. My results support many of the hypotheses which include aspects of biodiver-

sity beyond species richness alone, such as community composition and resource diversity. This indicates that restoration planning can be improved by incorporating both a food web approach and biodiversity-ecosystem theory. A food web approach will be useful for identifying key species whose presence or absence has strong influences on community structure and function, while theory can inform management objectives, such as whether to focus on restoring species diversity or functional diversity.

New questions

While my research indicates a food web approach is beneficial, it has also highlighted a critical gap in food web research: distinguishing the relative importance of functional, trophic, and species diversity in determining both food web stability and ecosystem function. In particular, further research on the roles and trade-offs of generalists and specialists within food webs is needed. There also need to be more empirical tests of these theories and models using real food webs. As I have demonstrated, food webs in impacted ecosystems may have already diverged sufficiently from the assumptions underlying many theories and models for their predictions to be applicable. For example, I found that eutrophic streams contained primarily trophic generalists, but was this because this configuration was the most stable under perturbation (enrichment), or because the systems had already degraded to an unstable state? Such questions are particularly relevant as we seek to maintain ecosystem stability and function in the wake of global biodiversity losses (McCann 2000).

Applications for stream management and restoration

The practical impetus for untangling the complex relationships within stream communities was to apply those insights to mitigate impacts of anthropogenic stress and restore ecosystems to a healthier state. My research has identified several key ways in which stream management and restoration can be improved.

At a broad scale, both management and restoration strategies focused on maintaining or restoring ecosystem function and stability will be more effective than biodiversity-based plans. Traditionally, stream restoration has relied on habitat improvements to increase biodiversity and thus functioning, but this approach has not been as successful as hoped (Palmer *et al.* 2010). Biodiversity-based strategies also often overlook biotic controls on ecosystem recovery, such as resource availability or trophic interactions (Lake *et al.* 2007). Process-based restorations are more likely to incorporate these other requirements because many ecosystem functions, such as energy flow, secondary production, and nutrient cycling involve both organisms and interactions (Lake *et al.* 2007; Thompson *et al.* 2012). Furthermore, the few studies, including mine, which have measured both structural (i.e. community composition and/or diversity) and functional responses to restoration have reported that functional metrics were more responsive to restoration than community measures (Brooks *et al.* 2002, Chapter Five). I found that common community and stream health metrics, such as the quantitative macroinvertebrate composition index (QMCI) were highly variable between streams and over time, and therefore may be less useful for monitoring restoration

progress than functional measures such as secondary production.

Focusing on maintaining or restoring functions should also address biodiversity versus community composition concerns. For example, if managers of eutrophic streams focus on improving energy flow and reducing trophic bottlenecks, they will be led to reduce the dominance of defended primary consumers, which will in turn improve community evenness, and possibly diversity as well. Of course, this approach may overlook taxa which do not serve a large functional role within an ecosystem (Palmer *et al.* 1997), but this could be secondary in degraded streams where communities are already simplified. When possible, managers should still aim to improve diversity, even within a functional approach, as functional redundancy is a key component of stability, and more diverse communities should therefore have greater capacity to resist future perturbations (Naeem 2002).

My research also indicates that degraded streams with highly simplified and isolated communities will require different tactics than streams which are still linked to more diverse regional species pools (Sundermann *et al.* 2011). Resource additions in healthy streams are predicted to increase diversity of invertebrates (Moore *et al.* 2004), whereas I found that restoring allochthonous resources in eutrophic streams initially increased dominance by fast-responding generalist taxa (Chapter Four), rather than alleviating exclusion of their competitors. In such situations, it may be necessary to actively remove or reduce dominance by problem taxa, such as defended generalist consumers (Wootton 2002; Davis *et al.* 2010) and re-introduce desired specialist taxa (if they were historically present at a given site).

To illustrate how these principles may be put into practice, I will outline some specific recommendations for mitigating eutrophication (summarised in Figure 6.2). Firstly, I would address the problem of dominance by defended and/or generalist consumers. This could be accomplished via several different strategies. Increasing stream shading will limit algal growth, thereby reducing herbivore populations (Stone & Wallace 1998, Chapter Four). While large-scale artificial shading is logistically impractical, planting riparian trees with large canopies will be an effective long-term solution (England & Rosemond 2004). Removing macrophytes, a preferred habitat for many more sessile invertebrates (Collier 2004), may help reduce abundances of defended taxa as well. Managed "floods" could also be used to periodically reduce defended consumer populations, as defended consumers are typically more susceptible to hydrologic disturbance than undefended invertebrates (Wootton *et al.* 1996). Because more mobile undefended taxa are able to take refugia during high flows and rapidly re-colonise following a flood disturbance (Lake 2000), such periodic disturbances could allow desirable species, such as EPT taxa, to re-gain a foothold. My results also suggest there is potential for top-down, or predator-driven, control of defended consumers; I found that upland bullies consumed defended consumers in highly productive sites (Chapter Two). However, like most other fish, the bullies still preferred undefended prey, which could result in greater suppression of desired taxa rather than defended taxa in restored streams. Further research on bully feeding preferences is needed to test this strategy.

Secondly, once dominance has been reduced, I recommend reintroducing allochthonous resources, either by direct additions of allochthonous material or by installing within-channel retention structures to collect leaves and form debris dams (Dobson & Hildrew 1992; Entrekin *et al.* 2008). Allochthonous additions will enhance secondary production and growth of desirable taxa,

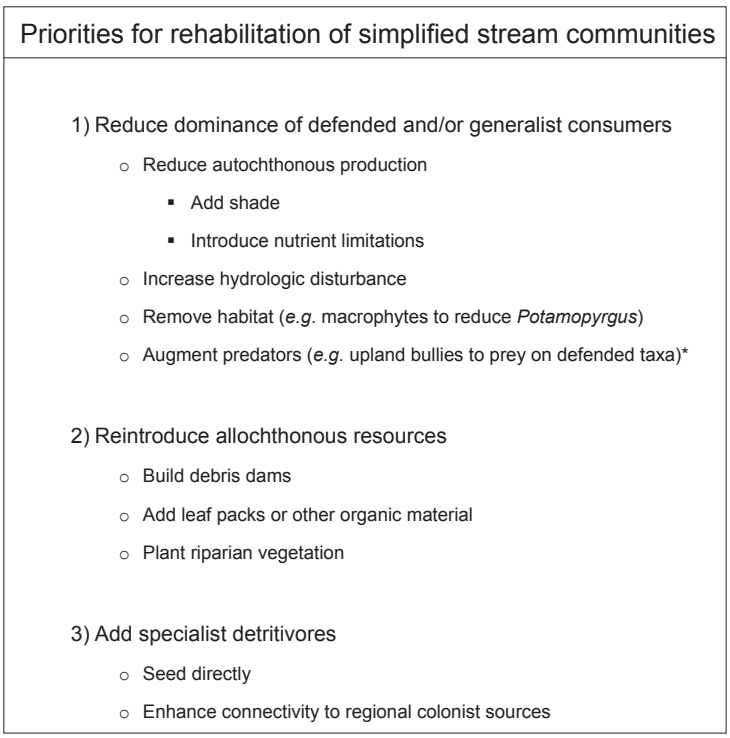

Figure 6.2: Guidelines for prioritising rehabilitation of highy degraded streams with simplified, predominantly generalist, communities. The * indicates a potential strategy that requires for further research (see main text for details).

such as *Deleatidium*, and further alleviate dominance (Chapter Five). Moreover, the addition of a second energy pathway will enhance food web stability (Rooney & McCann 2012). However, I suggest some additional investigation will be necessary to maximize the value of allochthonous resource restoration. Namely, it would be useful to test the relative effectiveness of single large resource additions, such as I used in Chapters Four and Five, with pulses of smaller additions. I observed that the short-term changes in community composition (Chapter Four) differed from the long-term effects (Chapter Five) of allochthonous resource restoration. This could be due to differential responses between taxa to varying conditions of leaf litter (Kominoski & Pringle 2009), or because short-lived generalist consumers increase production more quickly than larger, slow-growing specialists following increases in detrital resource availability (Cross *et al.* 2005, 2006). Further research on the timing of allochthonous additions may help managers more effectively target restoration efforts to specific desired taxa.

Thirdly, specialist taxa, such as detritivores, should be actively reintroduced following leaf additions. Detritivore additions will improve both community diversity and ecosystem function; because invertebrate detritivores contribute to the initial physical breakdown of leaf material, their reintroduction will also facilitate allochthonous resource use by other invertebrates and bacteria (Moore *et al.* 2004; Kominoski *et al.* 2010). Diversity of specialist taxa could also be promoted by focusing on improving the connectivity of the restored stream to a species-rich colonist pool (Parkyn & Smith 2011), although this is often difficult in highly developed areas where entire regional species pools are depleted (Sundermann *et al.* 2011).

Of course, which restoration strategy is ultimately chosen will depend on the objective of the restoration (Palmer *et al.* 1997), and will need to be adapted for each unique ecosystem. For example, if the aim of the project is to enhance biodiversity, then measures to reduce dominance will be crucial. However, if the goal is to improve ecosystem function, and the dominant species is capable of providing the desired function on its own, alleviating dominance may not be a primary concern. If the goal is to create more stable communities, then the focus should be on restoring diverse energy pathways, which may require alternative resource additions and increased species diversity. Restoration experiments are actually an ideal setting in which to continue testing and refining ecological theory on community structure and stability, such as the relative roles of generalists and specialists, as they provide opportunities for large scale manipulation of all levels of the food web (Palmer *et al.* 2006; Lake *et al.* 2007).

Conclusion

The research conducted in this thesis has contributed to our knowledge of the effects of eutrophication on aquatic ecosystems by identifying some of the mechanisms driving relationships between productivity, biodiversity, stability, and function in stream ecosystems. I have demonstrated that a food web approach provides the complexity required to understand and predict how stream communities will be affected by anthropogenic stress. My results show that shifts in community composition and structure associated with eutrophication in turn affect trophic interactions within food webs; the presence, position, and strength of these links determine food web stability and mediate the relationships between biodiversity and productivity. Furthermore, I have shown that restoring resource diversity can improve these linkages, thus potentially enhancing stability and function. However, both restoration success and diversity effects were limited by depleted species pools and dominance of trophic generalists. Although my work was conducted in a relatively small geographic area, I investigated an issue which is commonplace around the globe using general ecological concepts, and my results should be applicable internationally as well as within New Zealand.

Appendix A

Chapter 2 supplementary material

Supplementary methods

Gross primary productivity re-aeration measurement

Re-aeration in each stream reach was measured by propane evasion (Bott 2007). Propane was bubbled continuously into the stream along with a conservative tracer (rhodamine or sodium chloride) at the upstream end, and water samples for propane and rhodamine (or sodium chloride) were later collected at eight evenly-spaced stations along the reach once steady state (calculated as three times travel time) was reached. Propane samples were also taken at the same eight locations by collecting twenty-five milliliters of stream water with a syringe and injecting five milliliters of helium into that sample using a three-way stop valve. Samples were shaken for two minutes to fractionate the propane from the water into the helium, then propane samples were then taken from the gaseous headspace and injected into three milliliter glass vials which had been helium flushed and evacuated prior to sampling.

Propane samples were analyzed using gas chromatography (Shimadzu GC-2010 with FID detector, Shimadzu Scientific Instruments, Kyoto, Japan). When dilution had occurred along a reach, propane concentrations were corrected in proportion to changes in the conservative tracer concentration. The re-aeration rate of propane was calculated from the rate of propane decrease over the reach. This was then converted to oxygen re-aeration by applying an empirically derived conversion factor (Mulholland *et al.* 2005). For some streams it was not possible to detect a decrease in propane due to insufficient reach length. For those streams re-aeration was estimated from Odum (1956) night-time regression method.

Mantel test

To verify that our productivity gradient was independent of regional differences, we correlated dissimilarity matrices of principal component productivity variables and latitude and longitude coordinates for each site. We tested for correlations between the matrices using a Mantel test (based on Pearson's product-moment correlation) with 999 permutations in package 'vegan' in R. The Mantel statistic was 0.07908 with a significance of 0.147, indicating no spatial structuring of productivity variables.

Supplementary figures

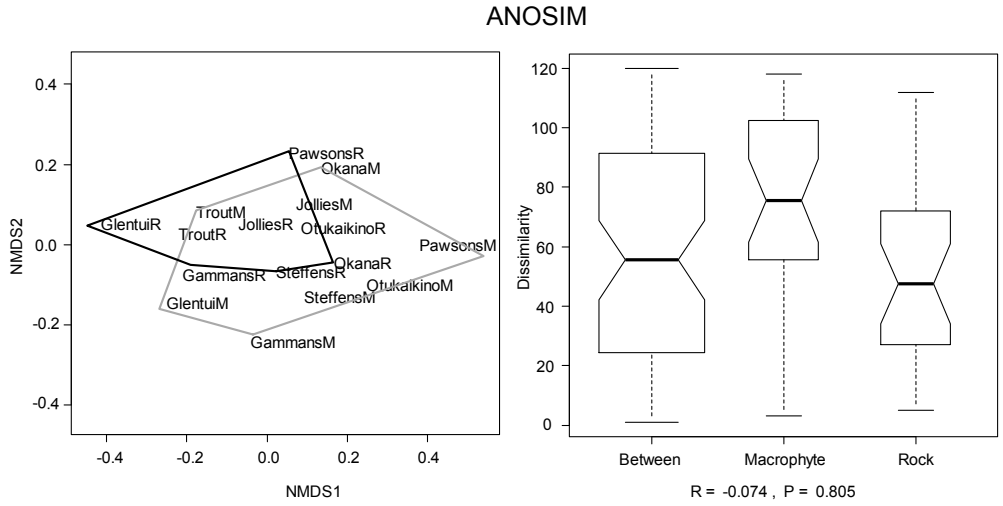

Figure A.1: a) Nonmetric Multidimensional Scaling (NMDS) and b) Analysis of Similarity (ANOSIM) for invertebrate communities from macrophyte and rock habitats. The NMDS displays the overlap in community composition; rock habitats are represented by the black polygon and macrophyte habitats by the gray polygon. The ANOSIM indicates that community variation was not significantly greater between habitat types than within each habitat type.

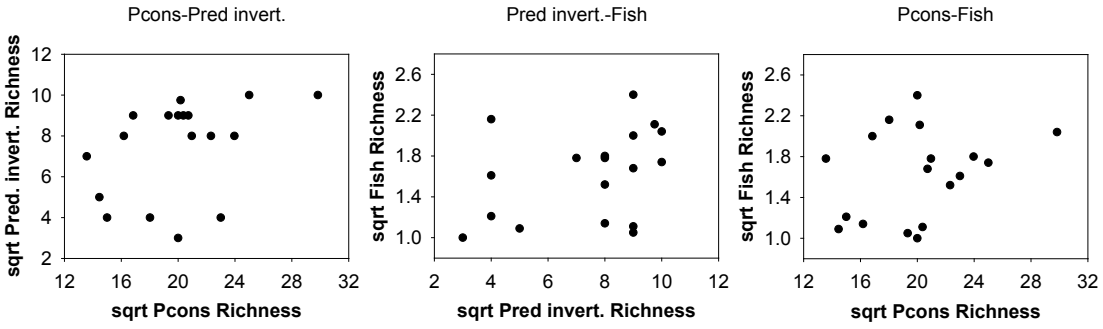

Figure A.2: Richness of each consumer trophic level in relation to richness of the other two consumer trophic levels. There were no significant correlations in richness between any of the three consumer trophic levels.

Supplementary tables

Table A.1: Ranges (minimum, maximum, mean, and median) of environmental variables and community composition metrics measured at 18 stream sites in the Canterbury region, South Island, New Zealand. Variables which were transformed for analysis are noted by [sqrt] or [log]; richness has been rarefied.

	Min.	Max.	Mean	SE	Median
Community metrics					
Richness (total) [sqrt]	18	42	28	1.45	29
Primary consumer richness [sqrt]	14	30	20	0.96	20
Undefended consumer richness [sqrt]	9	22	14	0.76	14
Defended consumer richness [sqrt]	5	10	7	0.34	7
EPT consumer richness [sqrt]	6	21	12	0.74	12
Predator richness [sqrt]	3	10	7	0.55	8
Fish richness [sqrt]	1	2	2	0.1	2
Abundance (total) [log]	2,782	166,253	44,090	10,005	34,967
Primary consumer abundance [log]	2,368	164,848	42,865	9,909	33,605
Undefended consumer abundance [log]	824	32,072	12,490	2,461	22,351
Defended consumer abundance [log]	752	139,936	30,376	8,754	9,979
EPT consumer abundance [log]	1,400	38,192	9,119	2,437	5,716
Predator abundance [log]	107	3,128	1,150	217	908
Fish abundance [log]	1	264	74.83	18.25	55
Environmental variables					
Chl-*a* (mg/m^2) [log]	6.29	46.22	18.9	2.51	17.27
NH_4 (mg/L) [log]	1.48	30.4	7.22	1.64	4.85
NO_3 (mg/L) [log]	0.01	8.5	1.18	0.65	0.04
PO_4 (mg/L) [log]	2.2	51.2	22.26	4.51	13.37
GPP (g O_2/m^2/day) [log]	0.04	2.78	0.62	0.21	0.24
Shade (%)	0	95	43	8.8	42.16
Macrophyte Cover (%)	0	85	19	5.68	11
Median Particle Size (cm)	0.01	16.5	5.36	1.06	4.25

Table A.2: Strength and significance of the non-metric multidimensional scaling (NMDS) ordination vectors. A significant *P* for the vector indicates an association between the ordination and changes in the vector variable. Positive strength values indicate a positive correlation and negative values indicate a negative correlation. For the NMDS, vector strength ranges from −1 to 1, with the strongest fits = |1|.

Community metric	NMDS1	NMDS2	*P*	R^2
Total richness	0.94	0.35	<0.01	0.56
Primary consumer richness	0.99	0.003	<0.05	0.45
Undefended consumer richness	0.99	0.13	<0.01	0.48
Defended consumer richness	0.02	0.99	>0.1	0.04
EPT richness	0.93	0.36	<0.01	0.5
Predator richness	0.11	0.99	<0.05	0.36
Fish richness	0.28	0.96	>0.1	0.09
Total abundance	-0.98	0.18	<0.001	0.56
Primary consumer abundance	-0.98	0.19	<0.001	0.55
Undefended consumer abundance	-0.81	-0.58	<0.01	0.58
Defended consumer abundance	-0.91	0.42	<0.01	0.46
EPT abundance	-0.31	-0.95	>0.1	0.11
Predator abundance	-0.88	-0.46	>0.1	0.19
Fish abundance	-0.64	-0.77	>0.1	0.22

Table A.3: Loading values for environmental variables in the principal components analysis (PCA), listed under the axis they were associated with. Variables were considered significant if the loading was > 0.7

Environmental variable	PC1	PC2
Gross Primary Productivity - GPP ($g/O_2/m^2/day$)	-0.861	
Percent macrophyte cover	-0.858	
Percent shade	0.801	
Median particle size (cm)	0.788	
Chlorophyll-*a* (mg/m^2)		-0.797
NH4 uptake ($mg/m^2/s$)		-0.743

Table A.4: Akaike Information Criterion (AIC_c) comparison of linear and nonlinear (quadratic) models for relationships between community variables and productivity measures. Non-significant pairings are not listed. A smaller AIC_c value is considered to be the better fit. Multiple models are compared using $\Delta AIC_c = AIC_{ci} - minAIC_c$. If $\Delta AIC_c > 2$, the alternative model(s) can be excluded.

	Productivity axis					
	PC1–GPP			PC2–chlorophyll-*a*		
	Linear	Quadratic	ΔAIC_c	Linear	Quadratic	ΔAIC_c
Richness						
Total						
Primary	21.62	23.27	1.65			
Consumers						
Defended				3.39	6.28	2.89
Undefended	15.87	17.96	2.09			
EPT	10.17	12.44	2.27			
Predators				23.07	25.3	2.23
Abundance						
Total						
Primary	57.51	55.63	1.88	63.47	65.96	2.49
Consumers						
Defended	65.42	64.48	0.94	67.49	70.37	2.88
Undefended	55.92	56.78	0.86			
Biomass						
Primary	49.35	50.08	0.73			
Consumers						
Defended	55.01	55.62	0.61			
Average weight						
Primary	40.64	41.3	0.66			
Consumers						
Defended	42.38	43.14	0.76			
Undefended	42.1	43.01	0.91			
Predators	38.13	39.22	1.09			
Fish	72.91	75.82	2.91			

Table A.5: Comparison of significance (P) between ordinary least squares regression and partial regression for each pair of community-environmental variables. Non-significant pairings are not listed.

	Regression			
	PC1 – GPP		PC2 – chlorophyll-*a*	
	OLS	Partial (PC2 constant)	OLS	Partial (PC1 constant)
Richness				
Total	0.02	0.02		
Primary Consumers	0.02	0.02		
Defended			0.01	0.01
Undefended	0.004	0.004		
EPT	<0.001	<0.001		
Predators			0.02	0.02
Abundance				
Total	0.004	0.001	0.08	0.02
Primary Consumers	0.004	0.001	0.08	0.02
Defended	0.02	0.005	0.05	0.01
Undefended	0.007	0.005		
Biomass				
Primary Consumers	0.06	0.04		
Defended	0.06	0.04		
Average weight				
Primary Consumers	0.01	0.008		
Defended	0.04	0.05	0.09	0.05
Undefended	0.05	0.04		
Predators	0.001	0.0009		
Fish	0.05	0.05		

Table A.6: Akaike Information Criterion (AIC_c) comparison of linear and nonlinear (quadratic) models for relationships between community palatability scores for fish and productivity measures. Non-significant pairings are not listed. A smaller AIC_c value is considered to be the better fit. Multiple models are compared using $\Delta AIC_c = AIC_{ci} - \min AIC_c$. If $\Delta AIC_c > 2$, the alternative model(s) can be excluded.

	Productivity axis					
	PC1–GPP			PC2–chlorophyll-*a*		
Palatability score	Linear	Quadratic	ΔAIC_c	Linear	Quadratic	ΔAIC_c
Fish						
Brown trout	39.86	41.93	2.07			
Canterbury galaxiid						
Longfin eel	39.67	40.31	0.64			
Upland bully				44.86	47.3	2.44

Table A.7: Comparison of significance (P) between ordinary least squares regression and partial regression for fish community palatability-productivity relationships. Non-significant relationships are not listed.

	Regression			
	PC1 – GPP		PC2 – chlorophyll-*a*	
Palatability score	OLS	Partial (PC2 constant)	OLS	Partial (PC1 constant)
Fish				
Brown trout	0.007	0.007		
Canterbury galaxiid				
Longfin eel	0.006	0.006		
Upland bully			0.07	0.06

Appendix B

Chapter 4 supplementary material

Supplementary tables

Table B.1: Linear mixed effects tests on pre-existing differences in community composition between treatment and control streams, and F-statistics and probability (P) for each comparison. All models were run with treatment as a fixed effect and stream as the random effect. There were three replicate measures (Surber samples) of each metric per stream.

Response variable	$F_{1,4}$	P
Abundance	0.01	0.94
Richness	0.4	0.56
Evenness	0.53	0.51
Berger-Parker Dominance	1.1	0.35
Percent EPT	1.67	0.26
QMCI	2.81	0.17
Chlorophyll-a	1.23	0.33

Table B.2: Standard deviations of intercepts for each final model, an indication of the relative size and influence of random errors in each model. Level is the level of nesting at which random effects were estimated, *i.e.* the lowest level of replication of the fixed effects included in each model. Stream is level 0, Shade is level 1, and Leaves are level 2.

Response variable	Level	SD model intercept
Algal biomass	1	1.11×10^{-1}
POM	0	6.17×10^{-2}
Abundance	2	1.15×10^{-5}
Richness	2	5.52×10^{-6}
Evenness	2	1.52×10^{-6}
Berger-Parker Dominance	2	1.45×10^{-2}
Percent EPT	2	6.37×10^{-2}
EPT Abundance	1	2.99×10^{-1}
QMCI	0	1.24

Table B.3: Linear mixed effects tests on differences in community composition between reach-scale leaf packs and baskets (un-shaded, without leaves, in order to minimize small-scale manipulation effects) in treatment streams, and F-statistics and probability (P) for each comparison. All models were run with sample type (*i.e.* leaf pack or basket) as a fixed effect and sample within stream as the random effect. There were three replicates of each sample type per stream.

Response variable	$F_{1,2}$	P
Richness	61.65	0.02
Evenness	4.84	0.16
Berger-Parker Dominance	0.32	0.63
Percent EPT	1.74	0.32
QMCI	0.63	0.51

Appendix C

Chapter 5 supplementary material

Supplementary tables

Table C.1: Length-mass regression equations, and sources, used to convert invertebrate body length (L, in mm) to dry weight (DW, in mg) for each taxon. Regression type refers to the form of the equation given; all forms are listed at the end of the table. a (or $log/ln(a)$ for transformed equations) and b are the coefficients for each regression

Taxon	Regression type	a or $\log/\ln(a)$	b	Source
Acari	2	2.02	1.66	Baumgartner and Rothhaupt 2003
Amphipoda	1	0.0058	3.015	Benke et al. 1999
Hydropsyche	2	-6.0016	3.0349	Towers et al. 1994
Chironomidae	2	-3.8757	2.7206	Towers et al. 1994
Deleatidium	2	-5.38	3.0555	Towers et al. 1994
Hudsonema	2	-4.894	2.4364	Towers et al. 1994 (Trichoptera)
Hydrobiosidae	2	-5.2103	2.2222	Towers et al. 1994
Oligochaeta	3	-2.618	1.875	Stoffels et al. 2003
Olinga	2	-6.5681	3.3417	Towers et al. 1994
Ostracoda	2	3.93	2.464	Anderson et al. 1998
Oxyethira	3	1.897	2.901	Stoffels et al. 2003 (*Paroxyethira*)
Physa	2	-4.74	3.21	Baumgartner and Rothhaupt 2003 (Gastropoda)
Platyhelminthes	1	0.0101	2.162	Benke et al. 1999
Potamopyrgus	2	-4.74	3.21	Baumgartner and Rothhaupt 2003 (Gastropoda)
Pcynocentria	2	-6.5681	3.3417	Towers et al. 1994 (*Olinga*)
Pycnocentrodes	2	-4.873	2.5024	Towers et al. 1994
Sphaeridae	3	-1.854	3.572	Stoffels et al. 2003

1) $DW = a * L^b$
2) $\ln(DW) = \ln(a) + b \times \ln(L)$
3) $\log(DW) = \log(a) + b \times \log(L)$

Table C.2: Cohort production interval (CPI) maximums and minimums (days), and sources, used in the secondary production calculations.

Taxon	CPI min	CPI max	Source
Acari	365		Di Sabatino et al. 2000
Amphipoda	365		Towns 1981
Hydropsyche	214	427	Huryn 1998
Chironomidae	66	365	Huryn 1998
Deleatidium	91	273	Huryn 1998
Hudsonema	329	730	Huryn 1998
Hydrobiosidae	138	824	Huryn 1998
Oligochaeta	365	730	Huryn 1998
Olinga	332	758	Huryn 1998
Ostracoda	90	120	Chapman 1963
Oxyethira	182.5		Towns 1981
Physa	365	395	Taylor 2003
Platyhelminthes	330	365	Huryn 1998
Potamopyrgus	365	730	Huryn 1998
Pcynocentria	243	609	Huryn 1996
Pycnocentrodes	243	609	Huryn 1996
Sphaeridae	395	425	Mouthon 2004

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